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ANIMAL BEHAVIOUR

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ANIMAL BEHAVIOUR

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EDITORIAL

Animal Behaviour

THE PRESENT ISSUE bears many features that distinguish it from its predecessors, not least being the change of title to *Animal Behaviour* and the addition of American colleagues to the editorial staff. These changes are the result of a liaison now established between British members of the Association for the Study of Animal Behaviour and their fellow workers on the other side of the Atlantic—a relationship which should prove fruitful to both. The first consequence is this much enlarged Journal which enables us to accept additional American contributions without reducing the publication facilities which were available to our original members. Moreover, the increased circulation which is another important consequence of the new liaison will ensure that the Journal becomes available to a wider circle of readers, and that discoveries on each side of the Atlantic will be more quickly appreciated on the other side.

It would be as well to trace in brief outline the history of the present series of publications, and of the means by which the new relationship has been established. The Institute for the Study of Animal Behaviour, as it was first called, was founded on 13th March, 1936, its declared aims being "to promote the study of animal behaviour, to encourage the undertaking of research into animal behaviour and the publication of the results of research, and to carry on such further activities as may from time to time be held to forward these objects." The first issue of the *Bulletin of Animal Behaviour* was issued in October, 1938, when the threat of World War II was already near. Two further issues of the *Bulletin* were produced during the war years, more frequent but still irregular publication began in December, 1947, and the series ran until March, 1951, when nine issues had been produced.*

It was already clear to members of the Association for the Study of Animal Behaviour, as it was now designated, that there ought to be a regular journal for the publication of original papers, but with a relatively limited, although growing, membership, means had to be found. The Association lent its scientific support to the new international journal, *Behaviour*. However, it desired its own publication, corresponding to those of other scientific societies, and so, after a period of negotiation—for which members remain indebted to James Fisher, their original Honorary Secretary—an agreement was concluded with the publishing house of Baillière, Tindall & Co. Ltd. and the first issue of the *British Journal of Animal Behaviour* appeared in January, 1953. Subsequent financial help from the Publications Fund of the Royal Society, and the full co-operation of our publishers, must be gratefully acknowledged.

It will be evident to our readers that, even from the first few issues, the designation "British" did not represent the whole activities of the new Journal. There has been a steady stream of contributions from countries outside the United Kingdom, and in particular from the United States. American workers have clearly felt for some years the need for a group equivalent in scope to the Association for the Study of Animal Behaviour, and some 18 months ago Dr. Martin W. Schein, Assistant Professor of Animal Behaviour at the Pennsylvania State University, and Dr. Lester M. Aronson, of the American Museum of Natural History, entered into correspondence with the Editors and outlined in detail the plans that have since taken shape for the formation of a Section of Animal Behaviour and Sociobiology of the Ecological Society of America. During 1957 Dr. J. P. Scott, first Chairman of the new Section, visited England and held helpful discussions with the Editor and Treasurer of the Association. The many necessary procedural details have been dealt with by the respective Committees and Officers, with the result that the new Section is now linked with the Association. An American Associate Editor, Dr. D. E. Davis, has been appointed, and various American members have been

*These issues are still obtainable, price 7s. 6d. each, from the Librarian of the Association for the Study of Animal Behaviour

selected, to join the panel of those who assist editorially. The Section has been granted equal use of space for publication of its proceedings, and so this issue contains abstracts of five papers sponsored by the new Section and presented at Indianapolis at the annual meeting of the American Association for the Advancement of Science.

Those who are concerned with the running of the journal are confident that these new arrangements, which in the first instance are to run for a trial period of 3 years, will work satisfactorily and will lead to stimulation of interest in the subject on both sides of the Atlantic. They wish it to be made perfectly clear, however, that contributions are to be welcomed from persons resident in any other country.

Every effort has been made during the five years that the *British Journal of Animal Behaviour* has been in existence to maintain high standards of acceptance for publication. In a subject such as animal behaviour, many contributions to which lie on the fringes of other branches of study, it is more difficult than in, say, physiology or biochemistry to fix definite standards or methods of presentation. Too rigid an approach might lead to the exclusion of papers that contain new and significant contributions. It is nevertheless of the greatest importance to the development of the subject as a whole that every reasonable effort be made to produce contributions that would be suitable, *ceteris paribus*, for other scientific journals of the highest standing. It is the earnest wish of the Association for the Study of Animal Behaviour and the Section of Animal Behaviour and Sociobiology that the standards already exercised in the case of the *British Journal of Animal Behaviour* should be maintained, and even raised, as *Animal Behaviour* develops.

Those on either side of the Atlantic who may wonder at the decisions to be taken in matters of spelling will be interested to know that, at any rate over the initial period, the American associates have generously suggested the adoption of British usage.

Since the study of animal behaviour is now a growing point in biology, psychology and animal husbandry, we are confident that *Animal Behaviour* will flourish and grow, as did its predecessors, although we may perhaps hope and expect that there will be no need for any further change in its title. In order to preserve continuity with the *British Journal*, this, the first volume of *Animal Behaviour*, is numbered Volume VI.

SYNOPSIS OF BEHAVIOUR TRAITS OF THE RING NECK DOVE

By WILMER J. MILLER and LOTUS S. MILLER

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A knowledge of normal behaviour of a species is of great value in interpreting results of experimental studies. For some purposes, it is desirable for a student to be free of preconceived ideas when he begins a study of natural behaviour. Nevertheless, it is useful in other cases to acquaint a worker quickly with the units of behaviour for any particular species so that he may go on to more advanced studies. This may be accomplished by concise descriptions of the voice, postures, and movements of a species of bird, for example, with a brief indication of how such traits fit into the general life history. Such an outline also would help other biologists and animal caretakers in handling and understanding their experimental animals. The following brief synopsis presents original observations on the ring neck dove, *Streptopelia risoria*, a domestic dove also known as Barbary or blond dove. The senior author has maintained reproductively active groups of this dove in captivity for the past fifteen years and has made continuous observations during six years on the large dove colony maintained by the Department of Genetics, at the University of Wisconsin.

The various displays and postures are grouped under six headings indicating the phase activity in which they occur. The units listed are heterogeneous but in a number of cases (e.g. B 1, 2, 3, 9 and C 1, 8) it seemed more prudent to group a number of related traits than to list each separately. The names are primarily descriptive but at times include reference to the situation of occurrence. An attempt has been made to minimize subjective interpretation in reporting observations; however, often it seems to indicate the apparent function of these movements.

A study by Craig (1909) on "emotion" in this species has been published. This work was stimulated by the earlier observations of Whitman (1919). Goodwin (1952) supplemented the earlier studies with a report on doves kept at semi-liberty, and presented comparative studies in 1956. The present authors were pleased to find so many points of agreement with Craig and Goodwin. There are a few minor areas of disagreement, but these are relatively unimportant to the present approach. In an outline such as this, it is difficult to indicate properly the sequence of postures in a given situation; therefore, the reader is urged to read the more fluent but less complete reports by Craig and Goodwin. Another pertinent study is that by Lehrman (1955) which is concerned mainly with parental feeding behaviour. A few disagreements of the present authors with statements in the latter paper have been reconciled by personal communication. The studies by Bennett (1939, 1940) on behaviour in ring neck doves are also interesting and significant, but are not pertinent to the approach of the present study.

This list of "unit" behaviour movements is not regarded as complete. For example, the authors are aware that parent birds may assist their young in hatching, resulting in a "T-shaped" shell breakage line. The frequency and details are not known sufficiently, however, to describe it satisfactorily.

A. Infantile and Juvenile Behaviour (in approximate order of development)

1. *Clutching.* The newly hatched squab clutches the nest sticks or the toes of its brooding parent with its feet, and hangs on tightly if disturbed. This behaviour persists until the squab is nearly fully fledged (about 3 weeks). It might serve in providing a solid purchase for the sometimes vigorous regurgitation-feeding (B 9).

2. *Head Waggle.* Very young squabs (decreasingly true for older ones) may shake or waggle the head as if the muscles were unable to properly manoevure the head. It apparently occurs when the squab is searching for food or seeking a new position.

3. *Squab Note.* Apparently when hungry, the squab will give a prolonged shrill, sometimes ascending whistle of low intensity. Rarely the whistle tends to descend the scale. The duration

*Paper No. 595 from the Department of Genetics, Univ. of Wisconsin, Madison, Wisconsin. Present address of the authors: Dept. of Veterinary Medicine and Dept. of Zoology, respectively, University of California, Davis, California.

is 1-3 seconds, but it may be longer in older squabs and repeated several times. It is usually accompanied by the squab wing shake (A 4) and bill searching (A 5). A very faint "peep" occasionally may be heard in the pipping egg, and the strength of this squab note increases with each day of growth.

4. *Squab Wing Shake*. The squab may shake its wings rapidly (perhaps two to four shakes per second) for a few seconds and repeat intermittently in food begging movements (A 3, A 5). It becomes increasingly obvious beyond the first week after hatching.

5. *Bill Searching*. Accompanying A 3 and 4, an older squab thrusts its bill towards the parent's body in rapid "wiggling" movements. The squab learns to aim at and thrust its bill near and into the parent's mouth (see B 9), but very hungry older squabs will thrust at the tail, rump, legs, or wings of the parent, the nest mate squab or even at their own wings. It may represent a more advanced form of the head waggle (A 2).

6. *Nest Defecation*. As the squabs grow they tend to back toward the edge of the nest to defecate. Not until the pin feathers are well developed do the squabs manage to defecate out of the nest.

7. *Bill Snapping*. Squabs and immatures may "click" or snap their bills one or more times when closely accosted by an unfamiliar object or movement. It develops rather suddenly (as the pin feathers open) as does the fight or flight stance (see D 4) which appears with bill snapping and hissing (A 8). Bill snapping may be given by nesting adults in an extremely soft version.

8. *Hissing* and *Puffing*. Squabs and immatures may fluff the feathers, especially those of the breast, and "hiss" when accosted as above. The wings may be raised as in the fight or flight stance (D 4). Nesting adults may express a faint hiss.

9. *Squeaker Notes*. Immature birds about four to eight weeks of age are termed "squeakers" by fanciers. Their voice is "squeaky", somewhat harsh and variable. As they become older, a similarity of the squeaker notes with the adult alarm note (E 6), "challenge" note (D 3) and the bow-coo (C 1) becomes evident.

(Reproductive maturity may occur from the end of the fourth month to the tenth month, averaging about six months. The voice is usually mature by the sixth month of age.)

B. Reproductive Behaviour (Non-sexual)

1. *Stick Nest Building*. (May belong with sexual behaviour C). Either sex, but more often the male, may walk around the ground picking up "suitable" (small, irregular shaped) sticks with its bill. Many sticks are discarded. The sticks are carried, a single stick at a time, to the nest site and placed near the partner. Usually, a longer section of the stick as held by the dove is carried projecting forward and down. Sticks beneath the nest site are ignored. The female predominates in arranging the sticks. However, a reversal of the roles occurs to some extent. Frequently the partner will "grab" the stick before it is placed and a short "tug-of-war" usually results. Juveniles have been observed to "play" with sticks.

2. *Egg Laying*. During oviposition, the female will stand and slowly raise the forebody. She appears to be straining for perhaps half a minute before the egg drops. She may ease the straining briefly and start again with a faint "ptk" expressed. During the straining period and especially near its termination, the eyes may be partially closed, or covered by the nictitating membrane. Also, the wings may droop, perhaps to assist the bird to maintain balance. As the egg drops, the head may be thrown up and back. The bird usually "rests" five to ten minutes standing over the egg before leaving the nest, or before starting incubation, if the second egg was laid.

(Usually the female will lay the first egg late in the afternoon and the second egg about 42 hours later. In this species a clutch usually consists of two eggs, occasionally one.)

3. *Incubation*. The parent crouches over the eggs, more or less orients them in a fore and aft position with the aid of the bill, the sides of the legs, and the keel, fluffs the ventral feathers which exposes bare skin, and then settles down on the eggs. Eggs in an unsuitable position may be retrieved by gently placing the bill over the egg until the egg can be rolled carefully underneath the bird.

(The female parent sets during the night and contiguous light periods. The male sets six to fourteen hours during the middle of the day, 9.30 a.m. to 4 p.m. being typical, the duration depending largely on the photoperiod. The length of the incubation period to hatching is 14 days).

4. *Faeces Retention*. During incubation, the faeces of the setting parent are retained until the

bird has departed from the nest, when a relatively enormous load may be released.

5. "*Hiding*." When closely approached either sex may remain motionless (crouch and freeze) on a nest of eggs or very young squabs. The head is drawn in and the feathers held tightly. This may be an alternative to the fight-or-flight stance (D 4) which also may be exhibited by a nesting bird. It is characteristic for any one bird to exhibit only one of these reactions in such a situation.

6. "*Squared*". When hiding (B 5) either sex may further tighten one wing (occasionally both) to the body so that the wing and back nearly form a right angle and tiny coverts near the shoulder are *not* smoothed to the rest of the wing but stand out.

7. *Broken Wing Ruse* or Injury Feigning. (Very rare.) When its nest was disturbed by the senior author, one white ring neck female clearly exhibited this behaviour common to mourning doves and other birds in which one or both wings are held awkwardly extended and shaken as the bird hesitatingly moves away from the nest site.

8. *Shell Removal*. After emergence of the squab from the egg, a parent frequently removes the two shell parts one at a time with the bill and flies some distance from the nest before dropping them.

9. *Regurgitation Feeding*. Either parent may feed one or both young together by opening its mouth and receiving the bill of the young in its bill. The parent usually lowers its head as it "pumps" food from its crop to the throat by violent "shivering" of the wings and crop. Nearly always the head is raised and the "pumping" process is repeated several times. Regurgitation feeding is sometimes initiated by a parent which may very gently peck or preen the newly hatched squab. During this process the head of the parent is often lowered and the bill partly opened. This pecking and preening usually stimulates the young squab to head waggle and bill search (A 2 and 5), although these may occur without detectable parental stimulation. See Lehrman (1955) for additional comments on this process.

C. Sexual Behaviour

1. *Bow-coo*. (The most frequent of coos.) The neck is inflated ventrally, the head and body held high; then the head is brought low suddenly with the bill pointed at or touching the ground. The pupil of the eye contracts. The first "note" of the call usually starts immediately as the head comes down. The first "note" is short; the middle notes form a rolling coo; and the last "note" is 2-4 times the duration of the first note, sometimes slightly descending the scale. If the observer is close, a strident, low, "appendix" note (one or two) is often heard at the end of the last note in the coo, as if the bird were regaining its breath or redistributing its air. The call may be indicated as huk' prrrroooo wah (wah). The bow-coo is always directed to or at a particular bird. It may be repeated as rapidly as 5 per ten seconds but usually a longer interval occurs between calls. One bow-coo averages about 2½ seconds per call. Between repeated bow-coos the male always "stamps" his feet lightly or steps toward the object-dove. However, sometimes one foot is only slightly raised and replaced. This call, occasionally given by unmated females, was never observed to be given by mated females.

2. *Perch-coo*. The notes are nearly the same as in a bow-coo (C 1), but they are given less hurriedly than the sometimes "frenzied" bow-coo. The perch-coo may be given with the eyes open, or nearly or completely closed and is the only coo also given at night. It is never obviously directed at any particular bird in sight.

3. *Nest-coo*. The notes of this call are nearly the same as in a bow-coo (C 1), but the call is softer, less forceful, and more intermittent. It is always accompanied by wing "flipping" (C 4). The head may "nod" at the beginning of each nest-coo. In a potential nest site males give this call more frequently than the female before a nest site is chosen, but afterwards the female may give it more frequently. (Apparently, doves sometimes consider a thin perch as a nest site and may even carry sticks to it, B 1).

4. *Wing Flip*. Either or both sexes in a nest site or more rarely on a perch may jerk their shoulders so that the wing, especially the tips, flip. Rarely only one wing is so flipped. Wing flipping may be constantly repeated and maintained intermittently for several minutes with a frequency of approximately two flips per second, Nearly always the head is held low and the tail high when the wingflip is given.

5. *Hetero-preening*. The male and female of a pair may "preen" each other, especially about the face and neck or head. Hetero-preening may be somewhat ritualised since the preening

movement is often more cursory than in homo-preening. Parents may hetero-preen their young, apparently assisting the feathers to break out of the sheath.

6. *Billing*. Billing occurs in a situation similar to hetero-preening (C 5). Billing is often initiated by the female which preens the neck and face of the male. After variable amounts of this hetero-preening the male may reciprocate and then take the bill of the female in his and apparently feed her as he would a squab. (It is not clear whether or not food is actually passed.)

7. *Sex-crouch*. The sex-crouch usually follows billing (C 6). The female squats, lowers her head, and raises her shoulders which will support the feet of the male.

8. *Sex-mount*. (Treading). The male's posterior feathers fluff out and he repeatedly "cranes" his neck above the female. He may "preen" or place his bill between his wing tips and rump. Then he mounts the female (both facing in the same direction) which is in a sex-crouch and maintains his balance by fluttering his wings. The tail of the male bends anterio-ventrally and swings from side to side until copulation. Normally, the sex-mount is always followed by the "laugh" or challenge note (D 3) by both sexes. The sex-mount takes about 5 to 10 seconds for completion, but the "preening" and "neck craning" by the male may be prolonged. Females very rarely try to mount mature males but may mount a partner frequently if paired with another female.

9. *Driving*. A few days prior to the female laying the first egg of a clutch, the male tends to follow her wherever she goes with occasional incomplete pecking movements (D 5a). Driving in ring doves is much less distinct than in *C. livia*. Goodwin (pers. comm., see 1956a) believes that driving normally occurs only if the potential sexual rivals are present.

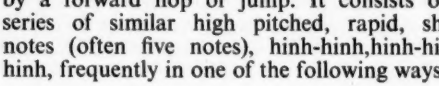
10. *Display Flight*. (see F 16d).

D. Aggressive Behaviour.

1. *Attack Posture*. The head is held low and horizontal and drawn close to the body. Sometimes the head is jerked up and down just before or after challenge notes (D 3) are given. The rump feathers are fluffed, and the pupil of the eye may contract and expand.

2. *Rush*. Maintaining an attack posture, the dove often runs or rushes at the opponent. At times the dove will fly toward the opponent but cage conditions tend to inhibit a rush by flying.

3. *Challenge Note:* Kah or "laugh." This note is nearly always given from an attack posture (D 1) and is often preceded or followed by a forward hop or jump. It consists of a series of similar high pitched, rapid, short notes (often five notes), hinh-hinh,hinh-hinh-hinh, frequently in one of the following ways:



They may ascend and descend the scale slightly or alternate notes may go higher; other combinations are more rare. The higher notes are accented. The challenge note given by a male often leads to bow-coos (C 1) if the "opponent" is a female and to a fight or flight stance (D 4) if the opponent is a male. Females usually give it only to newcomers, mates or territorial transgressors.

4. *Fight or Flight Stance*: Fear-threat display. A position nearly broadside to the opponent may be assumed with the wing opposite the opponent half raised. Initially the forebody is often raised slightly. Either escape (E 2, 3, 4, 5) or fighting (D 5a, b) may ensue from this position. It is especially easy to observe contrasting "intention" movements of the aggressive escape "conflict" within a dove in this posture.

5. *Fight*. (Intermittently accompanied by challenge notes, D 3).

a. Pecking. The aggressor dove pecks intermittently at the head, neck and shoulders of the opponent who may return pecks and wing blows.

b. Wing boxing. From the fight or flight stance (D 4) the opponent may be hit with single or multiple wing blows more or less directed to the head, neck and shoulders. It is the wing nearest the opponent which does the "boxing". Sometimes the opponent is hit by the wings of the aggressor in flight.

c. Standing on opponent. The aggressor often flies or hops to stand on the back of the opponent. Thereupon pecking or wing boxing may ensue; but strangely enough these are minimized and standing alone may satisfy the aggressor.

E. Escape Behaviour

1. *Alert Stance*. The body is held erect by straightened legs with the tail low, neck stretched

and the head high. The plumage is tightened close to the body. It is usually accompanied by the alarm note (E 6). The alert stance and the alarm note may be stimulated by the appearance of hawks, unfamiliar moving objects, or by humans, cats, rats, and snakes.

2. *Flight Stance.* The bird crouches, stretches the head forward, and raises the tail somewhat. It may follow an alert stance (E 1).

3. *Avoidance.* The head is held low and away from the attacker with the body in a crouch and sometimes leaning to one side; or, less often, the head may be held high, as the bird attempts to climb out of reach. It may be an intermediate form of the flight stance (E 2).

4. *Flight.* (See F 16). Outright flight often occurs immediately after an aggressor approaches, as when one dove is in another's territory. Flight usually terminates any persistent attack. When frightened from the ground by a hawk, the dove most commonly flies forward and upward with a noisy clatter of wings, according to Goodwin (1952).

5. *Wings Vertical.* Adults, juveniles or older squabs may spread the tail, fluff the feathers, and hold one or usually both wings vertically over the body which is sometimes inclined away from the attacker. It may follow a fight or flight stance (D 4).

6. *Alarm Note.* A soft "hinnnnh" may be given, often repeatedly. The character of this note may vary from time to time in the same individual, occasionally approaching a louder harsh quality. The latter may occur during feeding of the young. The duration of a single note is nearly one second, but a repeat note may be given every 5 to 10 seconds.

F. Other Behaviour

1. *Sun Bathing.* In direct sunshine, a dove may spread the tail, incline the body to one side and lift the wings, alternately holding one aloft during a few seconds or minutes.

2. *Water Bathing.* Doves may step into shallow water or sit on a perch near water level and fluff the feathers, crouch, and flutter the wings so that the water is "sprayed" throughout the plumage. The head is rapidly dipped or passed through the surface of the water a few times in a "sideswipe" motion. Often the wing is held vertical, but the tail is seldom spread. This response may also occur at the beginning of a light rain or spray of water. The bird always preens and shakes afterwards, if undisturbed.

3. *Relaxed Resting.* Beyond the usual "perching" a dove may lean its body to one side so that one wing is partly laid upon. Sometimes both wings are at an unusual angle (shoulders out, wrists in near feet). It occurs frequently in immatures and more rarely in adults.

4. *Stretch*

a. Gape. The neck is stretched forward and the mouth opened widely and moved forward and up.

b. Back Stretch. Both wings are held vertically over the body but *not* spread. The tail and head are depressed. It frequently precedes or follows a foot stretch.

c. Foot Stretch. (or foot and wing stretch). One foot and leg are stretched backwards; the tail and one wing are spread and extended toward the leg being stretched.

d. Upper Mandible Stretch. The terminal half (distal) of the upper mandible is sometimes lifted above the lower bill while the mouth is held closed.

5. *Rapid Peering.* The head is moved more or less up, forward and back in what appears to be visual "searching" movements. The head also may be turned from side to side allowing each eye in turn to see the object of attention.

6. *Questioning Bill.* When no escape behaviour is exhibited and when the bird is watching action or objects seemingly peculiar or unfamiliar to the bird, a "silent" rapid opening and closing of the bill occurs singly or repeatedly.

7. *Huddled.* When cold, ill, or "frustrated"(?) the bird may fluff the feathers, draw its head in very close to the body and perhaps even close its eyes. It may remain thus for hours in extreme cases.

8. *Shivering.* When very cold, ill or "ill at ease"(?) a shivering of the body and especially of the wings may occur.

9. *Sneeze.* The bird may be stimulated by illness or by unknown factors to "sneeze" in a sharp "pttk" accompanied by a sudden sideways jerk of the bill and head. If the bird does have a "cold," the sneeze may be followed by a wheezing sound.

10. *Preening* (homo-preening). The dove may arrange its feathers and their parts with the bill, each feather being passed between the mandibles in turn. A dove cannot reach its own head and many of the neck feathers for preening. The uropygial gland is used relatively infrequently.

11. *Ruffling and Shaking.* Practically all the feathers of the body are raised or "fluffed" and the wings and body are shaken vigorously. The feathers smooth down quickly afterwards. It often occurs during or after preening (F 10).

12. *Tail Wag.* Often after preening or ruffling and shaking or if an object drops on the bird's tail, the dove may shake the tail sideways somewhat like a duck but with only one or two shakes.

13. *Scratching.* The dove scratches its head and neck with its toes. The leg is not held dorsal to the wing as occurs in some birds when they scratch.

14. *Eye Wipe.* When a feather or foreign object adheres to the eye or when illness affects it, the dove may wipe its eye on its shoulder.

15. *Flight Exercise* or Wing Fanning. Immatures and adults after a period of relative inactivity may beat their wings somewhat as in flight but remain grasping the perch or at most hovering a few inches above the perch or floor.

16. *Flight*

a. Pen Flight or "hovering flight." The characteristic details of a dove flying in a pen or for short distances of a few feet have not been adequately distinguished. However, there seems to be a "hovering" quality distinct from distance flight.

b. Distance Flight. Since this species is usually caged, such flight is only rarely observed, but it is swift and direct according to Goodwin (1952).

c. Gliding Flight. The distance flight may be interrupted by gliding or sailing aspects with the wings held nearly motionless.

d. Display Flight. The male flies upward wing-clapping, then with the wings and tail spread widely he glides down, often in a half-circle (Goodwin, 1952). In wing-clapping, common in the domestic pigeon but less marked in the ring neck dove, the wings meet above the body in flight, producing a clapping sound.

17. *Defecation.* In normal defecation the vent feathers are fluffed, a semi-solid mass is expelled and the vent muscles are rhythmically contracted a few times.

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FACTORS AFFECTING THE LOCOMOTOR AND SETTLING RESPONSES OF ALATE APHIDS

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Introduction

Recent work on the behaviour of alate aphids has shown that they respond very differently to their host plants at different times. At the end of a teneral period following the final ecdysis they fly from the host plant on which they find themselves, although after a period of flight they may settle on the same or similar plant to feed and reproduce (Moericke, 1941). Aphids which were observed to alight on host plants in the field by Kennedy (1950) and Muller (1953) frequently left them again soon afterwards or after feeding on them for some time.

Moericke (1955) suggested that the adult life of alate aphids could be divided into four discreet phases in each of which the behaviour of the aphids was dominated by a different mood. These moods were the resting mood (*Ruhestimmung*), the flight mood (*Flugstimmung*), the attacking or settling mood (*Befallstimmung*), and the colonising mood (*Ansiedlungstimmung*). The resting mood existed after the final ecdysis and was due for the most part to the teneral condition of the insect which remained sitting on the plant until its cuticle and wings hardened. At the end of this period the aphids were believed to pass into the flight mood. Behaviour characteristic of the flight mood was seen in aphids taking off for the first time and consisted of apparent unresponsiveness to their host plants before and after taking off, and strong vertical flight when the aphids were airborne. "Tired and hungry" aphids (Müller & Unger, 1952) were believed to pass out of this mood into the attacking mood, flying horizontally and alighting on plants. Although they did not necessarily remain on the plants but frequently took off again, the aphids were believed to continue in the attacking mood and behave in a way which was distinct from their earlier behaviour while in the flight mood. The colonising mood occurred when the aphids settled down permanently, and their flight muscles then degenerated (B. Johnson, 1953).

Moericke's interpretation of the behaviour of alate aphids was accepted and developed by Müller (1953) and Müller & Unger (1951, 1952), but Kennedy & Booth (1950) were unable to confirm the existence of the sharp distinctions between the flight and settling phases through which the insects were supposed to pass, and believed that other considerations were more important in determining whether aphids feed or fly.

In the present study an attempt is made to analyse some of the factors affecting the behaviour of alate aphids from the final ecdysis until they have settled down on a plant and have lost the ability to fly.

Materials

Alate alienicolae of *Aphis fabae* Scop. from glasshouse colonies on *Vicia faba* L. and natural infestations of crops of beans, were used in the experiments. Aphids obtained from old colonies frequently showed a considerable variation in size; wherever possible undersized aphids were avoided.

Broadbean is a favourable host plant of *A. fabae*, and as it can be readily obtained at all stages of growth and in large quantities throughout the year it was chosen for most of the experimental work. The responses of the aphids were tested on mature leaves isolated from plants and kept in tubes of water, and on seedlings; these, representing relatively unattractive and attractive hosts respectively (cf. Kennedy & Booth, 1951). Fully expanded leaves were taken from the top half of plants about 18 inches high. The seedlings were 2-3 inches high. In some experiments the behaviour of the aphids was observed on a plant that was outside its normal host range, mature leaves of ivy (*Hedera helix*) being used.

Methods

It was necessary in the experiments to use aphids of as uniform age and history as possible. Teneral alatae, as far as possible of the same age as judged by the appearance of their wings, were collected in the evening and kept overnight

*This work was done at Rothamsted Experimental Station, Harpenden, Herts., England.

on host leaves in a dark cupboard in the laboratory. These aphids reached the end of the teneral period during the night, and by the following day had all spent a few additional hours on the leaves. This procedure gave aphids of an age and pretreatment resembling as closely as possible those of wild aphids constituting the first flush of take-offs in the day from a natural infestation (cf. Johnson, 1952). The treatment of the aphids differed from natural conditions in that the length of their exposure to darkness was prolonged, and the transition from darkness to light was sudden and unaccompanied by a slow rise in temperature as would occur in field conditions. There was no evidence that this procedure had the effect of producing any abnormal behavioural response in the aphids. To avoid disturbing all the aphids when some were taken for treatment, about 10-20 aphids were kept on each leaf. The leaves were kept under individual glass cases and were taken to the glasshouse in a dark box the aphids being taken out one at a time. Repeated opening of the door of the box caused some of the aphids to take off and fly to the glass cages over the leaves. As long as they were allowed to remain there for only a few minutes this had no appreciable effect on their subsequent behaviour.

A modified aspirator as described by Kennedy & Booth (1950) was used. The aphids were held by suction lightly against the hole which was applied to the wings or thorax; they could be picked up and released very quickly and easily by this method without damaging them.

The aphids were allowed flight exercise by two ways. Some were attached by the dorsum of the thorax to small pins and induced to vibrate their wings by a light puff of air; others were allowed untethered flight in a glasshouse. Aphids to be mounted on pins were held under a binocular microscope while a minute drop of watercolour paint was applied to the thorax with a fine No. 20 entomological pin with the tip of the point cut off; the pin was then quickly wiped clean and reapplied to the paint which rapidly hardened sufficiently to hold the aphid on it. The paint used was Windsor and Newton crimson lake tube watercolour. Watercolour paint has several advantages over other adhesives. It does not contain a solvent which could penetrate through the cuticle of the insect, the speed at which it hardens can be adjusted by varying its consistency, and it is very simple to detach the insect from the pin without injury. The aphids were released by pushing them off with a finger. In most cases they very readily dropped off the pin and they were allowed to fall straight on the leaf on which their behaviour was to be observed. The aphids could thus be picked up and attached to a pin in a very short time without using anaesthesia or cooling. The average time required to attach an aphid was only 30 seconds and to release it after flight took only a couple of seconds.

Aphids given tethered flight were flown in the glasshouse when the flight was of 5 minutes or less and were released straight on the leaves. Longer flights were given in the laboratory in a special chamber illuminated by a 200-watt lamp. The temperature in the chamber was maintained as near as possible to the temperature in the glasshouse to which the aphids were transferred immediately after they had been released on the leaves after flight.

Except where otherwise specified, aphids that were allowed untethered flight were put on leaves in the glasshouse and allowed to take off and fly to the roof of the glasshouse or of a 2′ 6″ high glass cage with a horizontal roof. If the aphids landed on the roof before they had flown for the necessary time, they were picked off and dropped to start them flying again. After they had flown for the necessary time, their flight was interrupted and they were put on a leaf.

It must be stressed that the aphids did not alight of their own accord. Thus, their experience was abnormal in that under natural conditions their behaviour on a leaf surface is preceded by the alighting response, whereas in the experiments they were deposited on the leaves after their flight had been interrupted artificially.

Behaviour Before Flight

The behaviour of young alate aphids at the end of the teneral period following the final ecdysis is very characteristic (Moericke, 1941, 1955). In favourable conditions for flight they move to the top of the plant or leaf and take off. If they are prevented from taking off by a wind, they persist in their attempts for long periods (Moericke, 1941) and will eventually take off in strong winds that earlier would have prevented them from taking off (Haine, 1955). If the aphids reach maturity during the night or under other conditions unsuitable for flight activity they remain with their stylets inserted into the plant but, although at this time they may contain a number of fully developed embryos, they do not reproduce (Johnson,

1954, 1955). If the aphids are transferred to bean seedlings as nymphs they behave in the same way on reaching maturity as they do on less suitable plants, and in suitable flight conditions take off without reproducing.

Aphids which had reached maturity overnight on bean leaves and seedlings kept in the dark cupboard were put in the light on the following morning. All withdrew their stylets and moved to the top of the leaf or plant and took off within a few minutes. When aphids were picked off leaves in the dark box and then put on fresh leaves or seedlings in the light they took off almost immediately.

Effect of Flight on Behaviour

The behaviour of aphids which were put on a host leaf after a sufficient flight was very different from their behaviour before flight. They did not attempt to take off straight away but probed the surface with their rostrum and wandered about for some time. This behaviour pattern is described in detail in a subsequent section (p. 18).

Under certain conditions which will be described later the aphids settled down on the host plant after wandering and probing and began to give birth to young. When this happened they could be said to be showing a stronger settling response than aphids which merely wandered on the plant and then took off again. Similarly, with aphids that did not settle down to reproduce, the length of time spent wandering on the plant was a direct measure of the strength of the settling response under the prevailing conditions.

A number of experiments were conducted in which aphids were flown for various periods from a few seconds to several hours and then released on bean leaves. The experiments were carried out over a number of days on which conditions were not always the same, wherever possible different treatments were compared simultaneously.

1. Tethered Flights of 10 Seconds and 30 Seconds

A number of aphids were attached to pins and flown for 10 seconds and 30 seconds. A control series of aphids was attached to pins but not allowed to vibrate their wings at all. The aphids were then released on bean leaves. The lengths of time they stayed are given in Table I. The unflown aphids nearly all took off straight away; all the aphids flown for 30 seconds went to the undersurfaces of the leaves and wandered for several minutes; of the aphids flown for 20 seconds, some took off straight away, some wandered for several minutes, while a number behaved in a manner intermediate between these and remained on the leaf for about one and a half minutes, making only one or two probes and moving only briefly to the undersurface. Two of the aphids which were not allowed to vibrate their wings at all also behaved in this way.

A similar experiment was conducted in which the behaviour of individual aphids was observed after successive "flights" of 0, 10, 20 seconds in which the aphids were attached to pins and released on to a leaf after each treatment. Seven aphids treated in this way stayed on the leaves an average of 18 seconds, 1 minute 30 seconds, and 7 minutes respectively after the "flights" of 0, 10, 30 seconds. These results were not obtained with all aphids: some took off immediately and others wandered for several minutes after the 10 seconds flight, but after the 30 seconds flight all aphids wandered extensively on the leaves.

Table I. Length of Time Spent on Leaves by Aphids "Flown" on Pins for 0, 10, 30 Seconds.

Treatment	Time on leaf (in minutes and seconds)							
Unflown	0·20 1·30	0·20 0·25	0·15 1·10	0·15 0·15	0·15 0·10	0·40 0·20	0·10	0·10
10 seconds flight	Short stay		0·30	0·35	0·25	0·30		
	Intermediate stay		1·20 3·30	1·20 1·20	1·25 1·10	2·15	3·20	1·30
	Long stay		16·25	11·55	8·30			
30 seconds flight	12·40 8·20	17·15 17·30	15·40 16·10		36·30 8·35	7·20 13·55	15·05 15·05	

2. Short Untethered Flights

Thirty to forty per cent. of a large number of alatae of *A. fabae* observed alighting on bean plants in the field by Müller (1953) took off again within a minute of alighting. It is very unlikely that the aphids had been airborne for less than 30 seconds before alighting yet they did not wander and probe on the leaves as the aphids in the above experiments had invariably done after 30 seconds flight. This suggests that the settling response was being produced in the experiments by a composite effect of flight and some feature in the experimental procedure.

Although attaching the aphids to pins and releasing them again without flight had no apparent effect on their behaviour, it was possible that flight while attached to pins was producing quite a different effect from free untethered flight, and that this was somehow responsible for their change in behaviour. As aphids almost invariably engage in strong vertical flight immediately after taking off, it was not possible to allow them an uninterrupted, untethered flight under controlled conditions before testing their response on leaves. Short untethered flights with less interference to their movements were obtained in two ways.

(*a*) *Cumulative Effect of Several Short Flights*

Aphids were allowed to take off from a leaf and fly to the sloping roof of the glasshouse. When they alighted on the roof they were rapidly picked off it and returned to the leaf. The aphids took off several times almost immediately on being put on the leaf, and after the next replacement wandered and probed for several minutes. The duration of each flight was timed with a stopwatch and recorded. The total flight before the changed behaviour occurred was obtained by adding together the several short flights. The results are given in Table II.

Table II. Duration and Number of Untethered Flights to Glasshouse Roof Necessary to Produce Changed Behaviour

	Average	Range
Number of aphids	50	
No. of flights/aphid	3·6	1-7
Duration of each flight	5·7 secs.	3-71 secs.
Length of flight to changed behaviour	20·3 secs.	

There was a fairly wide variation in both the number of flights undertaken by the individual aphids and in the total length of flight before the aphids showed the settling response. The average length of flight was 20 seconds and most aphids required less than 1 minute.

Between individual flights the aphids remained on the leaves for very short periods. Frequently they took off from where they were released, but mostly they crawled on the tip of the leaf and took off from there, but in neither case were they on the leaf for more than about half a minute and during this time they did not probe the leaf surface with their stylets.

(*b*) *Flight Against a Glass Pane*

When aphids take off in a chamber with a horizontal glass roof they fly strongly to the roof and then instead of alighting on it immediately as they do on a sloping roof, they may continue to fly with their antennae and forelegs against the glass for as long as several minutes before finally clinging to the glass and alighting on it. A number of aphids were allowed to fly in this way and were returned to the leaves with the sucker as soon as they stopped flying. In Table III, the aphids are divided into two groups: those which flew for longer than 20 seconds (but less than one minute) and those which flew for less than 20 seconds. The number in each group which wandered on the leaves for more than one minute is given.

Table III. Behaviour of Aphids after Short Uninterrupted Flights of More and Less than 20 Seconds, but Less than 1 Minute

	Less than 20 seconds	More than 20 seconds
No. of aphids	22	20
No. wandered on leaves	4	18

Few of the aphids which had flown for less than 20 seconds and nearly all the aphids which had flown for more than 20 seconds wandered on the leaves.

The results of these experiments indicate that aphids whose tethered or untethered flight was interrupted after about 20-30 seconds almost invariably showed the settling response of wandering and probing when put on a leaf. Aphids do not normally alight after so short a period and in fact they would not normally be in the proximity of any surface as they

Table IV. Length of Time Spent on Bean Leaf by Aphids Flown for 30 Seconds and 5 Minutes.

Length of stay	30 secs. flight		5 minutes flight	
	No. of aphids	%	No. of aphids	%
Less than 1 minute	4	3	0	0
1—5 minutes	30	21·3	0	0
5—10 minutes	53	37·6	6	15
More than 10 minutes ..	54	38·3	35	85
Total	141		41	

engage in vertical flight after taking off. The experimental procedure adopted therefore led to an abnormal situation and as a result of this the settling response was released.

3. Effect of CO_2 Knockdown

Dalmat (1950) and Ribbands (1951) found that light anaesthesia with CO_2 produced effects on the subsequent behaviour of *Simulium* flies and honeybees respectively. The settling response of alate aphids could be produced by giving them a knockdown with CO_2. A number of young alatae were taken from leaves kept in darkness and as they took off were put in a tube containing CO_2. As soon as they became inactive they were put on leaves. On recovering they probed the surface and wandered on the leaves before taking off again. Brief doses of ether did not have any effect on their subsequent behaviour and on recovery they became active and took off almost immediately without probing or wandering.

4. Activity Other than Flight

Müller & Unger (1952) followed by Moericke (1955) confined aphids in glass tubes after they had taken off and at various intervals replaced them on host plants. Many but not all of the aphids settled down on the plants after six hours in the tubes. Thus it was possible to produce the settling response by activity other than flight. This was also shown by de Fluiter (1949) who cut the wings off alate aphids and found that after a period of walking they eventually settled down. In the absence of flight a longer period of activity occurred before the settling response was released.

5. Flights of 30 Seconds and 5 Minutes

In this and subsequent sections it is shown that the strength of the settling response can be affected by the length of time the aphids have flown. Aphids were flown on pins for 30 seconds and 5 minutes and released on mature bean leaves. The results given in Table IV are from a number of experiments carried out over several days under various weather conditions.

The period for which aphids flown for 30 seconds stayed on the leaves varied from 0 minutes to about half an hour; only 38 per cent. of them stayed longer than 10 minutes. On the other hand all aphids flown for 5 minutes stayed longer than 5 minutes on the leaves, and 85 per cent. stayed longer than 10 minutes. It therefore appears that the longer flights resulted in more of the aphids staying on the leaves for longer periods than the short flight of 30 seconds, although it did not result in the aphids settling down on the leaves to feed and reproduce. All the aphids which had flown for 30 seconds and all but two of the aphids flown for 5 minutes took off within an hour.

In a further experiment aphids from a single batch were flown attached to pins in the glasshouse for 30 seconds and 5 minutes simultaneously. The aphids had been collected two days previously as tenerals and kept on bean leaves in the dark. The day after they were collected was overcast and cool and therefore unsuitable for experiments. The experiment was carried out on the following day which was clear, and the glasshouse temperature ranged from 68-75°F.

During the time they were in the dark some of the aphids had wandered off the leaves and were found on the walls of the glass cages over the leaves. These aphids were treated separately and were flown for 30 seconds. The length of time spent wandering on the leaves is given in Table V.

Of the aphids that had remained on the leaves while they were in the dark, none that

Table V. Length of Time* Spent Wandering on Bean Leaves by Aphids Flown for 30 Seconds and 5 Minutes.

	Length of flight	Time on leaves	Average
Aphids from leaf	30 seconds	3 4 4 5 3 3 3 3 3 3 3 3 5 5 2 3 4 9 8 7	4·1
	5 minutes	27 13 15 27 15 11 15 12 12 10 10	15·2
Aphids from cage	30 seconds	26 15 21 25 25 37 13 9 13 13	19·7

*To the nearest minute.

were flown for 30 seconds wandered for longer than 10 minutes before taking off again. Confinement on a host leaf in the dark for two days had therefore had no appreciable effect on their behaviour in the sense of weakening their locomotor response (cf. Haine, 1955). The aphids flown for 5 minutes all wandered for 10 minutes or longer thereby showing a stronger settling response than the aphids flown for only 30 seconds.

The aphids from the cage walls although flown for the shorter period also mostly wandered for more than 10 minutes, their average length of stay on the leaves exceeding that of the other two groups. It is apparent therefore that experience other than flight exercise (probably in this case starvation) can result in the aphids showing a stronger settling response.

6. Long Flights

If the length of time spent wandering on host leaves can be affected by the previous flight experience of the aphids, it should be possible by giving the aphids a still longer flight further to increase the settling response so that they either spend a still longer period wandering, or even settle down on the host leaves.

A number of experiments were carried out to investigate the effect of long periods of flight. Aphids were flown in a flight chamber indoors for periods of from 30 minutes to 4½ hours. After being placed on the leaves the aphids all wandered for up to about half an hour before either settling down or taking off again. Of the 161 aphids flown, 106 remained on the leaves long enough to deposit some larvae while 87 remained more than 3 hours, or overnight. The results are given in Table VI.

A higher proportion of aphids flown for 3-4½ hours (19 out of 22) settled down on the leaves for longer than 3 hours than aphids flown for 2 hours or less (68 out of 139), but as there was some variation between different experiments

Table VI. Behaviour of Aphids on Bean Leaves after Long Flights

Experiment	Length of flight in hours	No. of aphids	No. of aphids which reproduced	No. stayed overnight or >3 hours
A	½	10	4	4
B	½	21	17	8
C	1	10	9	8
D	1	6	4	4
E	1	16	10	8
F	1	6	5	5
G	1	6	3	0
H	1	10	3	0
I	1	3	1	1
J	1½	13	13	13
K	2	9	4	2
L	2	8	3	3
M	3	6	6	6
N	4½	8	5	5
O	4½	8	8	8
		161	106	87

% of aphids which produced one or more larvae: 66
% of aphids which settled down for more than 3 hours 54

it is not possible to draw any definite conclusions on the effect of long flights of different lengths. It is evident however that flights of ½-4½ hours resulted in more of the aphids settling down on the leaves either for long enough to deposit some larvae or for a few hours, than flights of only 5 minutes.

Table VII. Duration of Stay on Leaf in Seconds Between Successive Flights to the Glasshouse Roof

Experiment														
A	10	5	5	*70*	*400*	5	40	5	*600*	5	7	35	*120*	*500*
B	10	*200*	8	5	*360*	*80*	*480*	8	7	30	*510*	10	*250*	*260*
C	35	5	5	10	5	*360*	7	20	10	10	*350*	*600*	*300*	*410*
D	12	8	*180*	50	20	5	30	Settled down						
E	10	7	5	10	*120*	8	8	*150*	30	6	8	*250*	37	21
F	5	5	6	4	*140*	*270*	35	*540*	5	6	*600*	4	7	*120*

Figures which are in italics indicate that the aphids moved to the undersurface of the leaves and wandered and probed before taking off again.

The aphids did not remain on the leaves indefinitely. In fact most of them took off again the following morning, leaving behind batches of up to 15 larvae. So that after a period of recovery from the effect of the flight they again became unresponsive to the host leaves.

For each experiment a control series of aphids confined in a glass tube alongside the fliers and later flown for 30 seconds was kept. None of these aphids settled down on the leaves or remained on them long enough to deposit any larvae. To ensure that the long flight on the pins did not have a deleterious effect on the aphids, in some experiments half of the aphids which were flown for long periods were released on ivy leaves instead of bean leaves. The aphids all took off from the ivy leaves within a few minutes.

7. Transient Nature of the Effect of Flight

If Moericke's (1955) theory of phases is true and aphids which are responsive to host plants after some flight have entered a new phase in their life (*Befallsphase*) in which their behaviour differs from their behaviour before any flight at all, then it might be expected that all aphids which have at any time shown the settling response would behave differently from aphids taking off for the first time.

All of the aphids in the above experiments which had spent a period of wandering and probing on a leaf after a short flight, and most of the aphids which had settled down on a leaf for some time after a long flight took off again. They behaved then just as unflown aphids, that is, they were unresponsive to the leaves and took off repeatedly when replaced until they were again flown for more than 30 seconds.

A number of aphids of various histories were put on bean leaves and allowed to wander and then take off from them and fly to the glasshouse roof. After each flight they were replaced on the leaves. This was continued until the aphids had spent a number of periods wandering on the leaves. The individual flights generally lasted from about 3-5 seconds but after a few periods of wandering some of the aphids engaged in hovering flight when they took off and then remained airborne for up to 20 seconds.

The results of several typical experiments are given in Table VII. The length of each stay on the leaves is given in seconds. Aphids A and B had flown for one hour attached to pins on the previous day and had each produced 10 larvae overnight and taken off the following morning soon after being put in the light. The rest of the aphids had reached maturity overnight and were engaging in their first flight.

When the aphids took off again after the first period of wandering on the leaves they were as unresponsive to them as they had been before any flight at all: they had apparently completely recovered from the effect of their previous flight. The aphids which had flown for 1 hour on the previous day behaved in essentially the same way as the younger aphids.

After a few repetitions of the sequence of several short, followed by one long period on the leaves, some of the aphids settled down (e.g. D), and others stayed for long periods on each of several successive replacements (e.g. C) but did not settle down.

8. Loss of Effect of Long Flights

An attempt was made to find under what conditions the effect of a long flight could

Table VIII. Loss of Effect of Flight on Behaviour: Greenhouse Experiments

Length of flight	Aphids placed straight on bean		Aphids placed on ivy and then on bean after take off and 20 seconds flight.	
	No. of aphids flown	No. of aphids settled down	No. of aphids flown	No. of aphids settled down
1 hour	10	3	10	1
„	9	3	9	1
„	6	3	6	3
„	6	3	6	1
„	8	5	8	0
Totals	39	17	39	6

persist when the aphids were denied host plants when they stopped flying. Batches of aphids were flown on pins for one hour. Half of them were then placed straight on bean leaves as a control. The other half were released on ivy leaves from which they were allowed to take off, and their flight was then interrupted and they were transferred to bean leaves. Most of these aphids took off from the bean leaves straight away and were given a further 20 seconds untethered flight before being replaced on them. The results of the experiments are given in Table VIII.

In the control experiments a total of 17 out of 39 aphids which were placed straight on bean leaves after flight settled down on them for longer than 1 hour and deposited some larvae. Only 6 of the 39 aphids placed first on ivy then on bean (after a further 20 seconds flight) settled down on the bean leaves. It therefore appears that the long flight treatment ceased to be effective when the aphids were denied bean leaves straight after the flight.

The days on which the experiments were carried out were fine and hot and 1 hour's flight was insufficient to cause all the aphids placed straight on the bean leaves after flight to settle down. The slight tipping of the balance by a flight of 1 hour in favour of the aphids staying was easily upset by the interruption occasioned by their first encountering a non-host plant.

The experiments were repeated indoors in a specially illuminated cabinet and the aphids were allowed longer flights. The results are given in Table XI. More of the aphids settled down after having first encountered a "non-host" than in the previous experiment but fewer than of those placed directly on a host leaf.

Table IX. Loss of Effect of Flight on Behaviour: Indoor Experiments

Length of flight (hours)	Aphids placed straight on bean		Aphids placed on ivy and then on bean after take off and 20 seconds flight.	
	No. of aphids	No. of aphids settled down on bean	No. of aphids	No. of aphids settled down on bean
1	18	16	—	—
2—3	10	9	—	—
5	10	10	10	7
7	—	—	4	4
8	—	—	2	2
Total	38	35	21	14

In these experiments the balance was well weighted in favour of the insects staying: they had undertaken a long flight of 4-8 hours and the environmental conditions were less conducive to locomotory activity. It is interesting that even under these conditions first encountering a "non-host" apparently made some of the insects less ready to settle down on a host leaf.

Effect on Behaviour of the Surface on which Aphids are Placed

The behaviour of aphids which in the above experiments were put on host leaves after flight was not due solely to an increased responsiveness to the host, but also to a reduction in their readiness immediately to engage in further locomotory activity. This was demonstrated by releasing the aphids after flight on surfaces other than host plants.

1. Host and Non-Host Leaves

Aphids were attached to pins and flown for 30 seconds and released on paper "leaves" which were painted green, ivy leaves and bean leaves. A control series of aphids were attached to pins but not flown at all. The average length of time the aphids stayed on the leaves before they took off again is given in Table X.

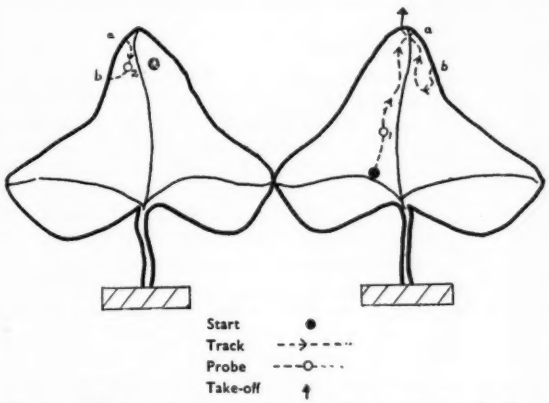

Fig. 1. Typical track of an aphid released on an ivy leaf after a flight of twenty seconds. (Left diagram, lower surface; right diagram, upper surface).

The aphids which had not flown at all took off straight away without wandering and without probing for more than 1-2 seconds. The aphids which had flown for 30 seconds all probed longer and wandered about on the leaves before taking off again.

Table X. Behaviour of Aphids on Different Surfaces after Flight

Type of leaf	No. of aphids	Length of time on leaf (Av.)	
		No. flight	30 secs. flight
Paper	2	20 secs.	1 min. 30 secs.
Ivy	24	20 secs.	2 min. 9 secs.
Bean	20	18 secs.	10 min. 15 secs.

The two aphids placed on the paper "leaves" each made two probes lasting an average of 15 seconds and wandered about at the tip of the "leaf" for a short while before taking off.

The aphids placed on ivy leaves after flight probed immediately or walked up the leaf for a few mm. and then probed. The probe lasted about 12-20 seconds. The aphids then continued to walk up the leaf until they came to the edge which they immediately crawled over onto the undersurface of the leaf where they often made a second probe. They then moved around at the tip of the leaf, returning to the upper surface and taking off again after an average stay of about two minutes (see Fig. 1). This type of behaviour was very similar to that shown by aphids flown for 10 seconds and then put on bean leaves (p. 11).

On bean leaves the aphids behaved at first in exactly the same way as the aphids placed on ivy leaves: they probed and crawled up the leaf and then over the edge to the undersurface. While the wandering on the ivy leaves had been confined to one or two turns at the tip of the leaf, on the bean leaves the aphids wandered for much longer mostly on the undersurface of the leaves and probed frequently. The pattern of behaviour was very uniform and aphids flown for more than 30 seconds did not take off again until they had been crawling about on the leaf for several minutes (Fig. 2).

In most of the experiments the leaves were isolated from the plants and had their petiole inserted through a hole in the cork of a 1" × 1" tube. The aphids frequently moved down to the bottom of the petiole in their wandering. Most of them, after touching the cork with their antennae, or stepping briefly onto it, crawled

up the petiole again. Some aphids walked onto the cork and remained walking around the edge of it for some time or walked down the glass onto the cage floor.

2. Different Stages of Growth of Host Plant

The behaviour of aphids was compared on three stages of growth of their host plant: mature leaves of broadbean, the growing shoot of young, healthy bean plants which were about 30 inches high, and bean seedlings which had only recently emerged from the soil.

(*a*) *Mature Leaves*

The length of time a number of aphids stayed on mature bean leaves after a flight of 30 seconds was given in Table XI.

The aphids wandered about on the leaves for periods varying from a few minutes to about half an hour; on no occasion when conditions were suitable for flight did they settle down on the leaves to feed and reproduce.

The duration of probes made during the stay on the bean leaves was recorded for several aphids. The length of the probe was measured from the time the aphid stood still and erected its rostrum until it lifted its rostrum from the surface of the leaf. The aphids generally only stood still when they were actually probing, the rest of the time they were on the leaf they spent walking about. It is likely in view of the observations of Bradley (1952) that the stylets are actually inserted in the epidermis of the leaf during these short probes.

Data on the length of stay on the leaf, number of probes and average duration of probes is given in Table XI, and the frequency distribution of the length of probe in Table XII. The average length of probe of 62 probes by 6 aphids was 16.2 seconds while the majority lasted 5-20 seconds. Very long and very short probes were infrequent. There did not appear to be any relation of the duration of the probe either to the different times the aphids remained on the leaf, or to the successive probes by the same aphids,

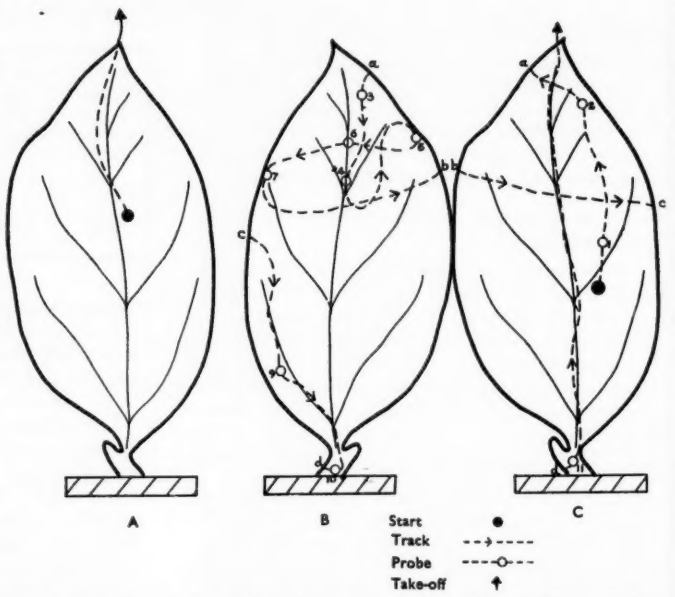

Fig. 2. Typical tracks of aphids released on a bean leaf. (A) Upper surface: before flight. (B & C) Lower and upper surfaces, after flight of twenty seconds.

(*b*) *Young Plants*

The top 8 inches of a young bean plant was cut off and kept in a tube of water. The cutting had three fully expanded leaves and the growing shoot intact. Twenty aphids were each given 30 seconds untethered flight and then released on one of the lower leaves. They immediately went to the undersurface of the leaf where they wandered about. Eventually they crawled off the leaf and along the petiole and stem to another leaf or the growing shoot. All the aphids wandered for 5-10 minutes (average 8.1) and took off again, except six which remained longer. Of these, two found their way into the tubular folds of the young unfurling leaves and settled down and remained overnight giving birth to 7 and 8 larvae respectively; the remaining four aphids stayed ½ to 1½ hours spending most of the time on the growing shoot where they deposited 1, 2, 1, and 1 larvae respectively.

Thus of the twenty aphids used, only six (30 per cent.) stayed long enough to leave any larvae at all. All of these aphids stayed on the young growing shoot of the plant. The failure of the rest of the aphids to stay any longer than they did may have been due to their failure in

Table XI. Number and Duration of Probes on Bean Leaf by a Number of Individual Aphids

Treatment	Time on leaf	Number of probes	Average duration of probes
1. Not flown	15 seconds	—	—
2. F 10 seconds	1½ minutes	1	12 seconds
3. F 30 seconds	6·5	7	12 „
4. „ „	6·55	11	13·3 „
5. „ „	12 minutes	11	19·7 „
6. „ „	12·40	8	27·4 „
7. „ „	16 minutes	16	15·7 „
8. „ „	19 „	15	13·5 „
Average length of probe			16·2 „

Table XII. Frequency Distribution of Duration of Probes

Length of probe	Frequency
1—5 seconds	5
6—10 „	13
11—15 „	26
16—20 „	10
21—25 „	3
26—30 „	6
31—35 „	2
36—40 „	1
41—45 „	1
>45 „	2
Total number of probes	69

their wandering before they took off again to find a suitable place to settle down.

(*c*) *Seedlings*

Sixty-one aphids were flown untethered for about 30 seconds and placed on young broad-bean seedlings less than 6 cm. high. The aphids were flown in six batches on different days all of fine warm weather. After a period of wandering all the aphids settled down and began to reproduce, except two which took off again after several minutes. The experiments were conducted in the morning and early afternoon and all except four of the aphids which settled down remained on the plant overnight and gave birth to all their first batch of larvae. The other four took off again after giving birth to 3, 3, 5 and 3 larvae respectively. Thus 55 aphids (90 per cent.) settled down on the seedlings and remained on them, and only 10 per cent. left them before they had given birth to all the larvae of the first batch.

The results of the experiments on the effect of the condition of the host plant on the behaviour of aphids after flight are summarised in Table XIII.

Table XIII. Behaviour of Aphids on Host Plants in Different Stages of Growth

	Number of aphids			
	Took off within 1 hour	Settled 1-6 hours	Settled overnight	Total
Mature leaves	50	0	0	50
Young shoot	14	4	2	20
Seedling	2	4	55	61

The effect of the condition of the host on the percentage of aphids staying and settling down on it is clearly shown. The aphids which settled down on the bean seedlings all remained on them until they had lost the ability to fly. The plants were kept undisturbed in the greenhouse. The aphids nearly all crawled into the small enclosed spaces in the furled leaves and growing

shoot, where they were almost completely isolated from the outside environment.

Movements on Plants

Before flight the behaviour of alate aphids is characterised by a strong positive phototaxis and negative geotaxis. If aphids are placed before flight on a pencil held vertically, they immediately turn to face upwards, crawl to the top of the pencil and take off. If they are replaced on it after a flight of about 30 seconds they very frequently move off in the direction they are facing whether this is up, down or around the pencil. If they are placed after flight on a leaf with its surface inclined at about 30° from vertical there appears to be more of a tendency to crawl up it whichever way they are facing. When they move to the undersurface they crawl over the leaf in any direction until they later return to the upper surface to take off. Thus, although there does not seem to be any persistent geotactic orientation after flight the insect does tend to "prefer" a position in which it is either upside down or vertical rather than the right way up, and when it is in this position it is negatively geotactic, although not strongly so. On the basis of these observations the wandering behaviour of alate aphids after alighting can be readily appreciated.

A number of sexuparae were placed after flight on a leaf on a stem of spindle (*Euonymus europaeus* L., the host plant to which they normally migrate) bearing eight other leaves. The aphids moved to the undersurface of the leaf and, after a period of wandering, crawled down the petiole and onto the stem. They almost invariably crawled on the undersurface of the petiole and therefore struck the stem facing down, and they proceeded to crawl down it until they came to another petiole and so crawled onto another leaf. In this way the aphids visited several leaves and on nearly every occasion on leaving the leaf they moved down the stem, so that finally nearly all the aphids finished at the bottom of the stem where it penetrated a cork. They did not walk off the stem onto the cork but turned about and crawled up the stem again. In this experiment the stem was held vertical; when it was held in a horizontal position the aphids did not move to the base of the stem.

On broadbean plants the situation is different. The petiole is thicker than that of the spindle leaves and has a stipule at the base. Aphids crawling down the petiole after wandering about on the leaf tend to be towards one side rather than in the middle and when they reach the base they crawl onto the undersurface of the stipule and from that depending on how and where they leave the stipule they go either up or down the stem.

Taylor (1955) observed that *Myzus persicae* landing on potato plants alighted generally on the upper leaves and that their wandering took them down the plants to the lower leaves where they often settled down. It would appear that the behaviour of these aphids was the same as described above for spindle and that it resulted in the aphids eventually getting onto the leaves they "preferred" at the base of the plant.

In *A. fabae* the preferred part of the bean plant is the growing shoot and it is interesting that the plant is so constructed that the aphids are not directed away from this as they would be if the plant had more of the characteristics of e.g. spindle or perhaps potato. These observations suggest that aphids alighting on plants may sometimes be directed away from their preferred region and then they may take off again after a period of wandering in which they failed to find a suitable place to settle.

Effect of Physical Environment on the Settling Response

1. After Flight

The environmental conditions prevailing after flight may materially influence the strength of the settling response of the aphids. This is shown in the following experiment in which aphids were put on mature bean leaves and kept in darkness for 24 hours *after* they had been allowed short flights on pins that in the light would only have resulted in the aphids wandering on the leaves for several minutes. Batches of aphids were flown for 0, 10, 20, 40, 80 seconds. The numbers of larvae deposited by the aphids by the following day are given in Table XIV.

A few of the aphids which had not flown at all, and a few of the aphids which had flown for 10 seconds had wandered off the leaves: those which had flown for these short periods and remained on the leaves were found the following day sitting at the tip of the leaf, and became active and took off as soon as the leaf was put in the light. Most of the aphids flown for the longer periods (40 and 80 seconds) were settled down feeding on the leaves and surrounded by their larvae; after a short time in the light they withdrew their stylets, moved to the tops of the leaves and took off.

Table XIV. Number of Larvae Deposited by Aphids Flown for Different Times

Length of flight (secs.)	0	10	20	40	80
Aphid number	No. of larvae				
1	10	8	13	12	12
2	2	8	11	12	11
3	1	6	9	11	10
4	0	2	8	11	10
5	0	2	6	10	10
6	0	1	2	10	9
7	0	1	1	10	9
8	0	0	0	8	8
9	0	0	0	8	8
10	0	0	0	7	8
11	0	0	0	0	8
Percentage of aphids which produced more than 6 larvae	9	27	45	91	100

A number of aphids flown in the same way and kept on non-host (ivy) leaves overnight did not produce any larvae at all.

The intervention of darkness immediately after the aphids had been put on host leaves after a short flight, had the same effect as a long flight of several hours, in that it increased the settling response so that the aphids settled down on the mature bean leaves to feed and reproduce.

2. In the Absence of Flight

If teneral alatae of *A. fabae* are put on host leaves which are then kept undisturbed in the dark, they remain on them but do not feed extensively (although they do insert their stylets) and they do not give birth to any larvae for at least 24 hours after reaching maturity. Aphids which are kept for longer than this, may then reproduce on the same leaves after being exposed to conditions which in younger aphids would have had no effect on their larviposition response.

Twelve aphids in the late teneral condition were placed on separate bean leaves and put in darkness and left undisturbed for four days. The temperature throughout the experiment ranged from 57-62°F. On the fourth day there had been no reproduction at all and the aphids were taken out of the dark and placed outside in the light where the temperature was 45-50°F, and left there for one hour. They were then returned to the dark. By the following morning all but two of the aphids had produced larvae. The numbers of larvae born were:

0, 0, 1, 3, 3, 5, 7, 9, 9, 9, 11, 13.

Thus, after four days without reproducing, sufficient stimulus to induce larviposition was obtained by placing the aphids in the light at a low temperature for one hour. The aphids remained and reproduced on the same leaves throughout the experiment.

Aphids which were subjected to similar treatment shortly after they had reached the end of the teneral period remained on the leaves but did not reproduce at all at least within the first 24 hours after being replaced in darkness.

From this and other work which will be published elsewhere, it is concluded that there is a lowering of the larviposition threshold with time. Aphids confined on host plants may therefore reproduce on them after a lapse of time without first engaging in any locomotory activity at all. Thus Kennedy & Booth (1950) were able to put young unflown alatae of *A. fabae* on broadbean seedlings and in "cool, dull, moist" conditions (which were apparently unsuitable for locomotor activity) the aphids remained on the plants feeding and reproducing.

In some species of aphids the larviposition response can be released more readily in the absence of activity than in others. Spring migrants of *Sapaphis mali* Ferr. transferred in the teneral condition from apple to plantain leaves (to which they normally migrate) and retained in the dark, almost invariably began reproducing on them within 24 hours of reaching maturity, whereas *A. fabae* retained on bean seedlings in the dark rarely produced any larvae in this time.

Discussion

The behaviour of alate aphids appears at first to be very complex, and in the past this has rendered their study difficult under experimental conditions (cf. Müller, 1953). In the present work this difficulty was largely overcome by employing an experimental procedure which temporarily eliminated the locomotor response of the insects, and it was then possible by varying other factors to determine their effect on the strength of the settling response that resulted.

A schematic representation of the kinds of stimuli affecting the behavioural responses of alate aphids is given in Fig. 3. The stimuli are shown affecting a higher nervous centre where they are integrated and where the type and strength of the response of the insect is determined.

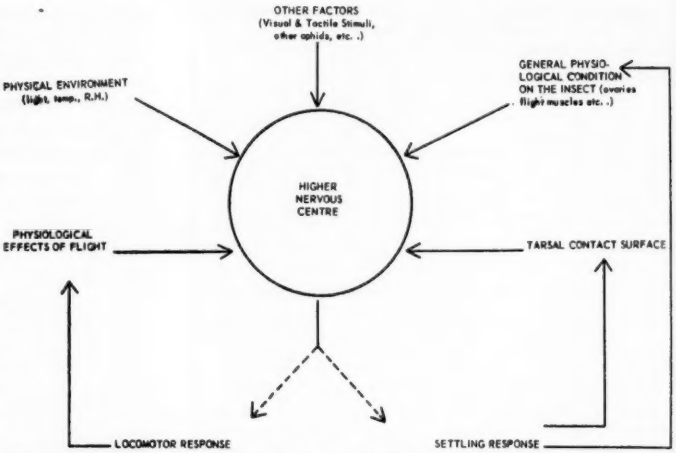
OTHER FACTORS
(Visual & Tactile Stimuli, other aphids, etc. .)
PHYSICAL ENVIRONMENT
(light, temp., R.H.)
GENERAL PHYSIOLOGICAL CONDITION ON THE INSECT (ovaries flight muscles etc. .)
HIGHER NERVOUS CENTRE
PHYSIOLOGICAL EFFECTS OF FLIGHT
TARSAL CONTACT SURFACE
LOCOMOTOR RESPONSE
SETTLING RESPONSE

Fig. 3. Schematic representation of stimuli affecting the behavioural responses of alate aphids.

It is suggested that whether alate aphids engage in locomotory or settling behaviour depends upon the nature and strength of the stimuli existing at any moment, rather than on any innate predisposition towards a particular kind of behaviour. The migratory behaviour of young alatae according to this view would owe its existence to the balance of stimuli favouring the locomotor response. The balance can shift and contra-locomotory stimuli may later increase in strength and result in the aphid showing the settling response. These stimuli can originate from the physiological condition of the insect or from its external environment. Aphids showing the settling response then continue to show it until the balance of stimuli no longer favours this response. Once the aphid shows the settling response its behaviour may lead towards providing stimuli which further strengthen the settling response such as feeding and larviposition and constancy of its visual field which would result from settling down on a plant.

The locomotor response and the settling response are mutually exclusive but each can become manifest in different kinds of behaviour. The settling response includes alighting, wandering and probing behaviour, feeding and larviposition, and the initiation of the physiological processes of which flight muscle histolysis is a result. Each of these phenomena can be regarded as a different degree of the settling response, since each involves a different level of physiological activity and each tends towards sedentary as opposed to locomotory behaviour. Alighting, and wandering and probing behaviour in themselves need have no permanent effect on the insect; feeding and larviposition involve processes of a more lasting nature although their effect on the aphids' behaviour is not necessarily permanent and irrevocable like the breakdown of the flight muscles.

The locomotor response consists not only of locomotory activity but also of a failure of the aphid to respond to its host plant when confined on it by conditions which are unsuitable for flight. Alatae of *A. fabae* remained for several days on bean leaves in darkness without reproducing, although they were never seen to remain on hosts for any appreciable time when suitable flight conditions prevailed (apart from aphids which settled down to feed and reproduce). Alatae of some other species, on the other hand, frequently spent a considerable time sitting on plants. One alate female of *Macrosiphum euphorbiae* remained on a potato plant for 7 days in suitable flight conditions in a glasshouse. At the end of this time it was given a short flight and returned to the plant where it then settled down straight away and within two days had lost the ability to fly. This type of behaviour of sitting on a host plant but not responding to it in the sense of showing some aspect of the settling response can be interpreted as a manifestation of the locomotor response, although at the time the insect is not actually engaging in locomotory activity.

The effect of both short and long flights on the aphids' behaviour was only temporary, but the effect of long flights persisted for longer than the effect of short flights. Aphids which were put on a leaf after a short flight took off again after a few minutes and subsequently

behaved just as aphids which had not flown at all. But, whereas aphids put on a non-host leaf after a long flight took off and behaved at first like unflown aphids, after a further short (20 seconds) flight they showed a much stronger settling response than aphids which had had only short flights. Thus stimuli originating from the residual effects of the insects' previous experience, although they did not bring about the settling response, persisted in the insects and were capable of strengthening the settling response when it did occur. It is possible that such a situation would not occur in nature and that it may be in that sense an artefact due to the experimental conditions. It is interesting however that it does occur at all and it indicates that even in the presence of a strong physiological "need" of the insect to settle down (such as that produced by starvation or exhaustion) the insect may still show locomotory behaviour. A further example of this will be given. It was a frequent experience when handling alate aphids to find that aphids which had spent several hours off their host plants either in cages or in the glasshouse, when put on plants flew from them straight away. If these same aphids were then allowed a short flight of 20 seconds and returned to the plants they showed a strong settling response, some even feeding and reproducing.

Müller's (1953) observation that a high proportion of alatae of *A. fabae* alighting on bean plants in the field took off again without wandering on them whereas, almost without exception, the aphids used in the above experiments wandered after a short 20-30 second flight, suggests that some feature in the experimental procedure was affecting the aphids. In the absence of any flight at all, or after short sub-liminal flights handling the aphids had no effect on their behavioural response. When aphids alight on leaves they frequently give the impression of being torn between the settling response and the locomotor response (cf. Müller, 1953). At this time they are very sensitive to their environment and whether they proceed to take off again or to wander and probe on the leaf can be influenced by apparently irrelevant stimuli—such as the sudden inversion of the leaf, or a slight decrease in light intensity; Müller (1953) suggested that the higher temperature at the leaf surface than of the surrounding air at the time of his observations might have been responsible for the aphids taking off again so readily. It is possible that in the experiments described above the interference with the normal activities of the aphids provided an additional stimulus that led to their always showing a clear settling response but that it was only effective after the aphids had had a flight of about 20 seconds.

The effect of flight on the behaviour of the aphids might occur through the accumulation of some metabolic products. The fact that a few seconds flight had such a large effect may have been partly due to the rapid build up of CO_2 in the initial few seconds of flight due to a lag in the effectiveness of the flight respiratory movements and the higher metabolic rate associated with the strong flight that follows take off. The persistent effect of longer flights might be accounted for in terms of oxygen debt. It is not suggested that the aphids would only remain settled down as long as there was an oxygen debt but that this could be an important influence in causing them to settle in the first place. How long they remained settled down would depend upon other factors.

There is also some evidence of the persistence of the effects of the insects' previous experience within the nervous system. The same behavioural response occurred when aphids which had been flown for 20 seconds were released, irrespective of the nature of the surface they were put on. But their subsequent behaviour varied considerably on the different surfaces: on host seedlings they settled down, while on paper and non-host leaves they soon took off again. This suggests that, as the aphids took off immediately from *all* surfaces before flight, there had been a persistence of the effect of flight beyond the first few minutes after it had been terminated. But because the aphids stayed for such different times on the different surfaces, and as only a very short flight was sufficient to result in the settling response, it is unlikely that the persistent stimulus was from outside the nervous system but rather that it was some kind of residual nervous excitation.

The theory first suggested by Moericke (1941) and supported by Müller (1953) and Müller & Unger (1952) that the life of alate aphids while they are capable of flight is divided into two distinct phases, a dispersal phase and an attacking phase, is not substantiated by the experiments reported above. The principal evidence given in support of this theory is that aphids which were observed taking off from plants they had alighted on did not fly strongly upwards as they did when taking off for the first time, but engaged in hovering flight and prob-

ably alighted again soon after taking off. It was shown above (page 15) that aphids taking off from host leaves both after short periods of wandering after flights of 20 seconds, and the following day after a long flight of 1 hour and after depositing a number of larvae, behaved in essentially the same way as aphids taking off for the first time, in that they engaged in strong vertical flight and they showed a weak settling response when returned to host leaves after repeated short flights of 20 seconds. As Moericke and Müller & Unger based their observations on aphids which had recently alighted, it is possible that the aphids were still being influenced by the physiological effects of their recent flight, and if they had settled down on the plants for longer periods, their behaviour when they took off again would then have been the same as for aphids which were taking off for the first time.

Aphids are weak fliers in that they are incapable of horizontal flight of a speed exceeding 2-3 m.p.h. Kennedy (1950) has stressed that their dispersal is active and not passive in the sense that they actively launch themselves and actively alight. But while they are airborne they may have relatively little or no control of their movements depending on the velocity of the air mass they are in. Their dispersal therefore depends upon launching themselves and then entering a moving air mass: this they could effect by flying strongly upwards as soon as they are airborne, and then maintaining hovering flight. After a brief period of strong flight some insects (e.g. locusts, Weis-Fogh, 1952) settle down to a more steady but slower flight, and aphids appear to behave in the same way. Although aphids are very small, and therefore difficult to keep in sight when they are airborne, a number observed taking off in a sheltered garden were seen to climb strongly for about 15-20 feet and then begin to hover. Moericke (1955) and Müller & Unger (1952) believed that aphids not engaging in vertical flight were in the attacking mood. But hovering aphids do not alight on all plants they are confronted with and are frequently seen hovering near plants but making no attempt to alight on them although they are apparently incapable of distinguishing host from non-host plants before alighting (Kennedy, 1950). It seems unlikely therefore that the change from vertical to hovering flight is normally associated with any change in the aphids' predisposition towards alighting, but that as alighting is a manifestation of the settling response it is elicited by stimuli of essentially the same kinds as those shown above to affect later manifestations of the settling response.

Some species of aphids appear to be more "restless" than others (Kennedy, 1950). One of the causes of this may lie in the relative abundance of host plants of the different species and in their adaptation to this. Where the host plants are rare, the aphids will generally have to fly for a longer time to find them than aphids with plentiful host plants, and they will then probably settle down on them. Where host plants are abundant, the aphids will be able to be more discriminating and only remain on those plants which are very suitable, or only settle down and remain on plants after they have spent some time flying from plant to plant and depositing larvae on several (Johnson, 1953). The less suitable the host plants are for permanent colonisation the more "restless" the aphids will be before settling down. An aphid with a very wide host range such as *Myzus persicae* has abundant host plants, but all the plants within its host range are not equally attractive to it, in fact most of them are not sufficiently attractive to induce permanent settling; so it becomes a particularly "restless" aphid in that it spends more time flying, wandering and spending short periods of feeding between flights, than aphids with less abundant or more suitable host plants. This type of behaviour is particularly suited for the transmission of plant viruses.

The host preferences of alatae of *A. fabae* were studied by Kennedy & Booth (1951, 1954) who confined aphids in small cages containing leaves and after various periods counted the numbers of aphids which were settled and feeding, and the numbers of larvae produced. The experience of the aphids prior to the experiments was not uniform and differed both between different individuals in the same tests and between the batches of aphids used in the different tests. As a consequence the aphids showed little uniformity in their behavioural preferences although there were "tendencies" for the aphids to prefer certain kinds of leaves. As the strength of the settling response of aphids can be influenced after flight by the nature of the surface they are put on, the method of comparing the behaviour of aphids on leaves either after a short controlled flight or after a knockdown with CO_2 should be useful in studying their host preferences. By

standardising the age and experience of the aphids used it should be possible to obtain an accurate expression of differences in preferences of the aphids for different hosts.

Aphids and locusts appear to have a number of features of their biology and migratory behaviour in common. In both insects the production of migratory individuals is generally the result of an excessive population build up accompanied or followed by deteriorating conditions for the maintenance of the population. In aphids those conditions result in the determination before or shortly after birth, of alate forms. In locusts the individuals subjected to crowded conditions can respond by developing into the migratory form, although the extreme form generally requires more than one generation. Both aphids and locusts then exhibit behaviour which is characterised by locomotory activity and a relative unresponsiveness to apparently suitable places to settle down to feed and reproduce. In aphids it is relatively easy at least experimentally to terminate this migratory activity, and once it is terminated, given certain conditions, the insect reverts to a sedentary existence which continues for the rest of its life. Kennedy's (1956) recent biological theory of locust phases can apply also to apterous and alate aphids where the juvenile (in the sense of non-locomotory) character of apterae is even more a conspicuous feature than the juvenile character of solitary locusts, due to their failure to develop wings which are typically adult structures.

Summary

In suitable environmental conditions for flight, alate aphids typically fly from their parent host plants and they can not normally be brought to settle down on those or other plants until after they have engaged in flight or other activity. In unsuitable flight conditions they remain on the plants but do not respond to them by feeding and reproducing. Aphids alighting on plants after flight normally spend some time wandering and probing and they may settle down.

By allowing young alatae of *Aphis fabae* Scop. short tethered and untethered flights of a minimum of 10-20 seconds and then putting them on a leaf surface, it was possible to induce wandering and probing behaviour. There is evidence that aphids do not normally alight and show this behaviour after being airborne for such a short time, and the behaviour of the aphids in the experiments was probably due to the composite effect of flight and some part of the experimental procedure. Wandering and probing behaviour could also be produced by giving aphids a knockdown dose of CO_2, and by allowing them an extensive period of activity other than flight.

The length of time aphids spent wandering on plants before they took off again, and whether or not they settled down to feed and reproduce, was influenced by the length of flight they had engaged in, the nature of the surface they were released on, and the physical environment. Aphids flown for five minutes or less and put on mature host leaves in the light wandered and probed but soon took off again; aphids released on host seedlings or on mature leaves which were then put in darkness, after short flights of a few seconds, and on mature leaves kept in the light after long flights of 30 minutes to 8 hours, frequently settled down to feed and reproduce.

The effect of both short and long flights was soon lost and in the absence of strong contra-locomotory stimuli such as darkness or a very suitable host, the aphids reverted to typical locomotory behaviour after showing some degree of the settling response (i.e. wandering and probing or settling down for some time).

Much of the behaviour of alate aphids can be grouped under two opposing general responses: the locomotor response and the settling response; it is suggested that the stimuli determining the type and strength of response of aphids at any time are principally of the same kinds as those which were shown in the experiments to affect the strength of the settling response.

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STRIDULATION AND ASSOCIATED BEHAVIOUR IN CERTAIN ORTHOPTERA. 2. STRIDULATION OF FEMALES AND THEIR BEHAVIOUR WITH MALES

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Introduction

The previous paper in this series (Haskell, 1957) described the stridulation of the males of certain grasshoppers and their behaviour towards each other. The present paper describes the stridulation of females and their behaviour in relation to the stridulation of males. Data on hearing in females of the experimental insects which is relevant to the present work has been published elsewhere (Haskell, 1956 a & b).

Materials and Methods

To enable comparative studies of behaviour to be made, experiments were carried out with the females of a group of four closely related grasshoppers of the sub-family Truxalinae (Dirsh, 1956), namely *Stenobothrus lineatus* (Panz.), *Omocestus viridulus* (Linn.), *Chorthippus parallelus* (Zett.) and *Chorthippus brunneus* (Thunb.) (=*C. bicolor*, Charp.). The collection and culture of the insects and the equipment and method of studying their behaviour was as described in the previous paper. The nomenclature of the songs and the terminology used in the analysis of stridulation is also as in the preceding paper.

The grasshoppers used were divided into a number of groups each of which differed in its history and treatment. Each group was given a code figure which summarised the treatment of the insects in it. A list of these code numbers and the treatments to which they refer are now given in order that future reference may be made by using the code number only.

Stenobothrus lineatus

Group B: a mixed group of males and females, originally collected at all stages and ages, which were allowed to live and breed together normally.

Group NB: a group of females only, collected in the 2nd and 3rd instars, segregated from males and not allowed to mate during captivity.

Omocestus viridulus

Group B: as for *Stenobothrus* Group B above.

Group NB: as for *Stenobothrus* Group NB above.

Chorthippus brunneus

Group B: as for *Stenobothrus* Group B above.

Group R: a group of females, collected at all ages, not allowed to see males or hear their stridulation during captivity, and in the "responsive state" (see page 28) to male normal song.

Group S/M/S: a group of females, collected in the 2nd and 3rd instar, kept from sight or sound of males, which had been allowed to copulate to completion once and were then isolated again.

Group S/UM/S: a group of females, collected in the 2nd and 3rd instar, kept from sight and sound of males, who were unwilling to mate when paired with males, and who were kept in isolation.

Chorthippus parallelus

Group R: as for *C. brunneus* Group R above.

Group S/M/S: as for *C. brunneus* Group S/M/S above.

Group S/M/B: a group of females, kept isolated until in the "responsive state", then allowed to mate under controlled conditions and kept in breeding cage with males thereafter.

As regards food supplies, temperature, hours of light and dark, all the groups were kept in as nearly identical conditions as possible. Apart from these groups, which consisted of from four to twelve insects, various other treatments were given which will be described in the text.

Each insect in every group was individually marked with coloured paint spots on the pronotum for purposes of recognition, and during the course of the work each female was

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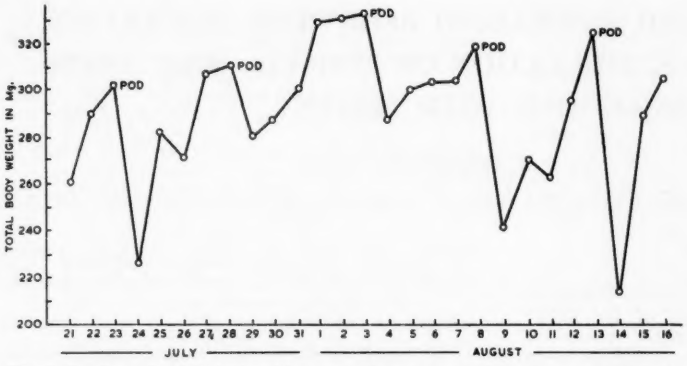

Fig. 1. Portion of weight/oviposition curve for an *O. viridulus* Group NB female.

weighed daily. The weight of a female, when plotted against time, showed small individual variations from day to day and larger variations correlated with oviposition. Fig. 1 shows a typical weight/oviposition graph derived in this manner. These weight curves made it possible for various types of behaviour to be related to the position of the insect in its oviposition cycle, following the interpretation of Richards & Waloff (1954) on mean mature weights and the weight changes correlated with oviposition in these grasshoppers. Occasionally large changes in the weights of some insect occurred which could not be related to oviposition, but generally these could be shown to be due to some disturbing influence such as temperature fluctuation in the cage or temporary lack of food; insects near such weight changes in their cycle were not used for behaviour experiments.

Results

One of the main difficulties in work on the responses of female grasshoppers to the natural or recorded song of the males has been, hitherto, the extreme variability of the results, and the fact that an insect which responded unequivocally to a stimulus one day, gave no response 24 hours or even 2 hours later. The present work shows that this variability lies in physiological changes which occur in the females and affect their responses to acoustic stimuli; a technique for obtaining females in a state in which they were responsive to male normal song was discovered, and use of these responsive females in behaviour experiments enabled variations in response patterns and the effect of various acoustic stimuli to be investigated in a more detailed manner than in previous work.

During the investigation it was found that females which respond to male normal song do so with stereotyped behaviour patterns. This stereotyped response pattern, which is basically the same for all four species used in this work, will be referred to as "typical behaviour" in this paper, and a female giving "typical behaviour" responses on stimulation by the normal song of a male of its own species is said to be in the "responsive state".

In order to condense the lengthy descriptions of behaviour which would otherwise be necessary, the section dealing with each species begins with a description of "typical behaviour" between males and females when the latter are in the responsive state, and is followed by an account of experiments which verify this initial statement and demonstrate the variations of typical behaviour which occur in each species under various circumstances.

Stenobothrus lineatus

Typical behaviour in this species is as follows. A male begins singing the normal song; a responsive female within range will orientate towards the source of sound, and may give a short burst of response stridulation. After this, it will move towards the male, sometimes pausing to stridulate and often pausing to reorientate. When within visual range of the male, it moves right up to the latter and when within 5 to 7 cm. stops and stridulates. The male, on seeing the female or hearing her stridulate or both, stops singing the normal song and, with or without various transitional phrases, begins the courtship song and finally leaps on the female; the genitalia being engaged, no further stridulation is made unless the female moves, or the pair is otherwise disturbed, when the male sings the copulation song (Haskell, 1957).

Although both Groups B and NB of this species were kept for over a month and their weights indicated they were mature, very few of them oviposited; because of this, behaviour could not be readily related to position in the

PLATE I

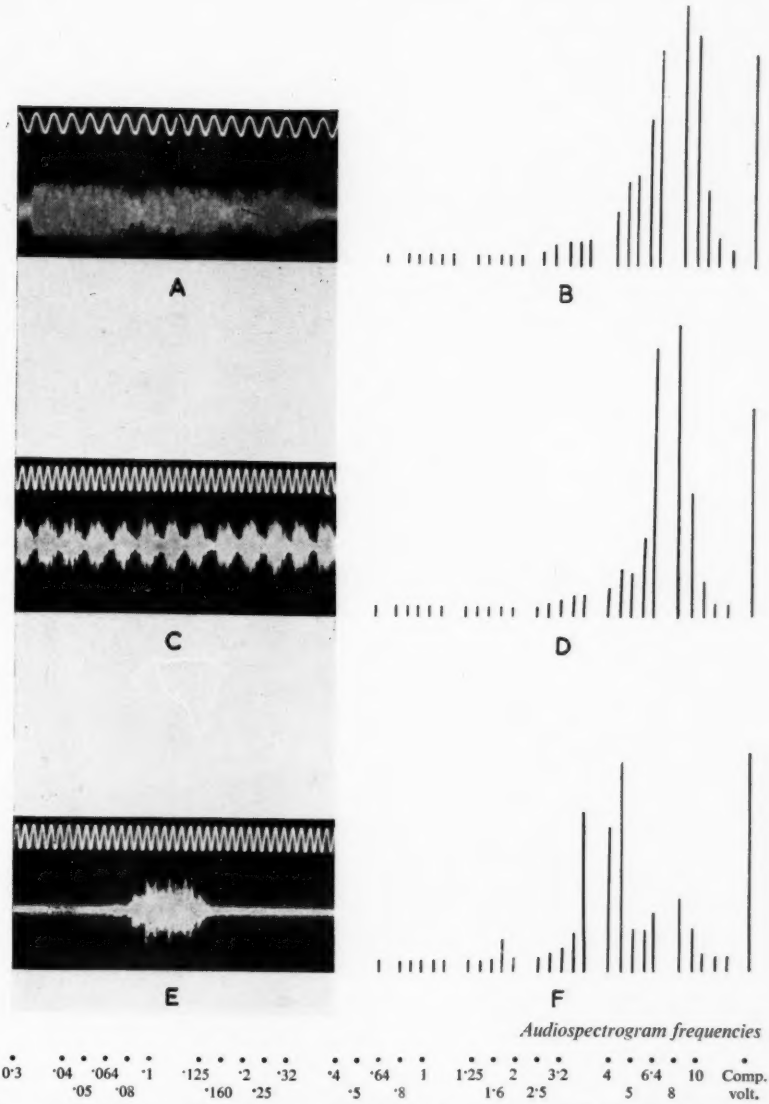

Fig. 2. Oscillograms and audiospectrograms of female stridulation. In the oscillograms the timing wave is 50 c/s and in the audiospectograms the mid-point frequency of each band is shown in k/cs, the line at the extreme right being an orientation deflection from a 1.5 volt. battery.

A, B, *Stenobothrus lineatus;* C, D, *Omocestus viridulus;* E, F, *Chorthippus brunneus.*

oviposition cycle, and therefore no special group experiments were done with this species However, during an observation period of 35 days, three copulations by Group B females were observed, while in Group NB introduction of males to the cage for one hour daily over this 35-day period led to 12 copulations. Typical behaviour in response to male normal song was only elicited from females of Group NB who were prepared to let males mate with them. Such females would also orientate to and move towards a loudspeaker emitting a recording of the male normal song.

During some of these experiments, certain females stridulated in response to the male song, and this stridulation was recorded and analysed. Fig. 2 (A & B) shows an oscillogram and audiospectrogram of the sound. The movements of the hind femora of the female resulting in production of this sound were very similar to those of the male when the latter emits the normal song, but the movements of the female were much more jerky and the sound was emitted in short bursts.

Omocestus viridulus

Typical behaviour in this species is as for *Stenobothrus lineatus*. Group B mixed breeding group of 8 females and 10 males was observed daily for 28 days and during this time only four females were found in copulation. At the end of this time, all the females were segregated in a cage isolated from the sound of male stridulation. They were tested for response to male stridulation and willingness to copulate by putting males in the cage for an hour each day. For the first six days of this experiment all attempts by males to mate were refused and no reaction to their stridulation was observed. After six days, one female allowed a male to engage the genitalia; the pair was separated immediately this occurred. On successive days an increasing number of females showed typical behaviour in response to male normal song and allowed males to engage the genitalia, but no copulation was allowed to proceed beyond this initial stage. The results of this experiment are shown graphically in Fig. 3. One female was never seen to allow any male to mate with her.

Group NB females were much readier to mate than those of Group B. Over a period of 39 days, during which time adult males were put in the cage for one hour daily, a total of 34 copulations by 12 females was observed. These matings were never allowed to go to completion,

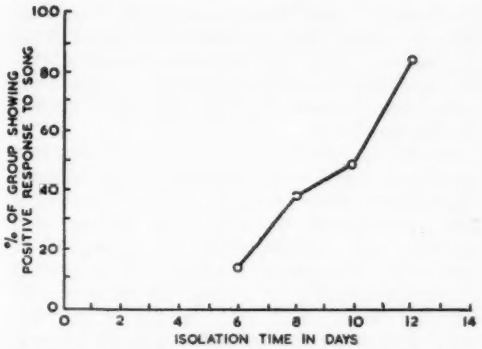

Fig. 3. Increase in positive response of *O. viridulus* Group B as a function of isolation time.

the insects being separated as soon as engagement of the genitalia showed that the female was ready to mate. Females which responded to the natural song of the males would also orientate to and move towards a loudspeaker emitting a recording of the male normal song. During these tests it was observed that females would not respond to natural or recorded male normal song when within 24 hours of oviposition, but recovered the response soon after oviposition had taken place.

During these observations, several females stridulated in response to male song while in the initial stages of searching for the male. This song was recorded and Fig. 2 (C D) shows an oscillogram and audiospectrogram of the sound. This is very similar indeed to the male normal song and the movements of femora during the production of the sound seemed very like those of the male.

Chorthippus brunneus

Typical behaviour in this species is of two types; in the first type, the behaviour is as described for *S. lineatus*. The difference between this and the second type lies in the fact that in some cases when a female stridulates in response to male song, the male orientates towards the female and moves towards her. Sometimes the female moves after stridulating and sometimes it does not; in the latter case, the male eventually finds the female, but this is rare. Most often a mutual search is made, with both insects making short stops for alternate stridulation.

In Group B of this species no copulation was observed during a 56-day observation period.

Playback of male normal and courtship song did not elicit any locomotor or stridulatory response from females, nor did artificial stridulation, although occasionally some of the males in the cage responded to these stimuli by singing the normal song.

In Group S/M/S all the seven females had mated once and were thereafter kept solitary. Males were put in the cage for one hour every day, commencing the day after mating, and reactions were observed over a period of 19 days. Fig. 4 is a graph showing the percentage of females ready to permit copulation (the criterion being that they should permit the male to engage the genitalia) plotted against

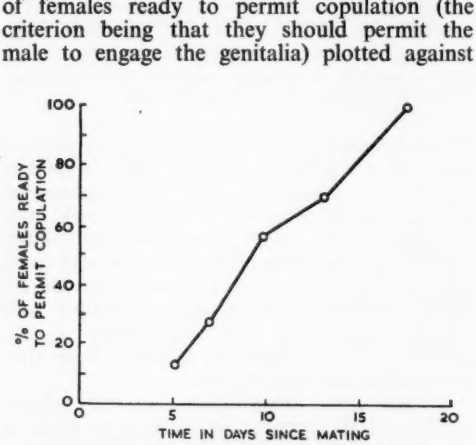

Fig. 4. Percentage of *C. brunneus* Group S/M/S ready to permit copulation as a function of time in days since last mating.

time elapsed since mating. No mating was allowed to proceed to completion in this experiment; as soon as a female was seen to have allowed a male to engage the genitalia, the pair was separated and the female removed to a separate cage for the remainder of the daily observation period. At the end of the 19-day observation period of this group, all females would permit copulation and five out of the seven would emit their response stridulation as soon as a male began to sing its normal song. However, it was observed that on occasion some of these five females did not respond to the male song, nor would they permit copulation; it was found that the response was absent about 24 hours before, or during, the day on which the insect oviposited. One of the insects was tested in detail for this inhibition of response over a period of 21 days and Fig. 5 summarises the results of this experiment.

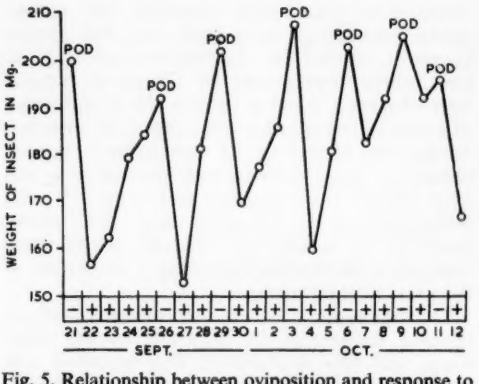

Fig. 5. Relationship between oviposition and response to male song in a *C. brunneus* Group S/M/S female. +, responsive; —, non-responsive to song.

The responsive females of this group were placed in a cage with a number of *C. brunneus* males which had had their tegmina removed so that they were incapable of stridulation. Subsequent observation over a period of seven days showed that only one copulation took place. Males encountering a female would make stridulation movements with their hind femora, but were always repulsed when attempting to engage the genitalia.

Group S/UM/S females were collected as 2nd or 3rd instar nymphs and on moulting to adults were put with males, but refused to mate. Daily trials with males showed that the refusal to mate was kept up over a period of time, which varied with the individual, but generally ceased at about the time of maturation. The data from this experiment are summarised in Table I. This group of females was then tested daily for

Table I. *C. brunneus* Females Group S/UM/S: Time of First Mating

Insect no.	Number of days between final moult and first mating	Weight at first mating in milligrams
1	12	188
2	13	223
3	14	218
4	12	178
5	13	217
	Average 12·8 days	Average 204.8 mg.

a further seven days by introducing adult males into the cage for one hour daily; all five females remained responsive to male normal song and would permit copulation to start. The response was absent, however, in females 24 hours before they oviposited but was recovered shortly after this. At the end of a week the group was placed in a cage with an equal number of mature males; all five soon copulated and this was allowed to proceed to completion. The mixed population was then observed daily for a further week but no further mating took place and no response could be elicited from the females to the natural or recorded normal song of the male. At the end of this week the females were removed to an isolated cage and were tested daily for response to male stridulation. This was done by placing a single male in the cage and making this sing in response to artificial stridulation (Haskell, 1957). Fig. 6 shows the increase in the percentage of the group responding to stridulation plotted against the length of time elapsed since removal from the

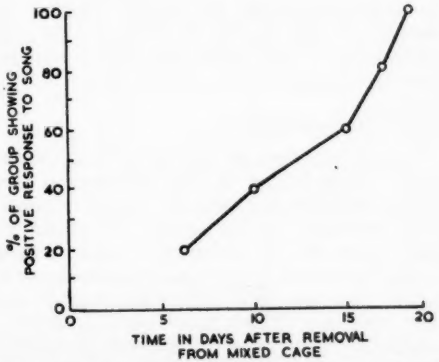

Fig. 6. Percentage of *C. brunneus* Group S/UM/S showing positive response to male song as a function of time elapsed since removal from mixed cage.

mixed cage. That this response to male stridulation also coincided with a willingness to mate was shown by placing the females in a cage with males, when copulation was permitted by all the females after the usual stridulation responses; this copulation was not allowed to proceed, the pairs being separated and the females removed.

Three of these responsive females had slits made in both their tympanic membranes and the air sacs behind the drums were also pierced. Haemolymph exuded from the puncture and after several hours coagulated around the scolopale sensillae and rendered the organ quite insensitive to sound. This operation had the advantage over extirpation of causing less operational shock and less water loss. Electrophysiological preparations of the tympanal nerves of these insects at the close of behaviour experiments confirmed that their tympanal organs were insensitive to airborne sounds. After a recovery period of 24 hours in their solitary cage, the three treated and two untreated females were once again returned to the cage containing males, and the latter induced to stridulate by artificial stimuli. The two untreated females responded with typical behaviour, while none of the treated insects responded in any way and vigorously rejected all attempts at copulation. The two untreated females were not allowed to copulate fully, but were removed and deafened in the manner described above. They were kept isolated for 24 hours and then returned to the cage with the other treated females and a number of males. During this 24-hour period no copulation was observed by the three previously treated females, and during a subsequent three days' observation of all five treated females no reaction to male stridulation was noticed and copulation was refused by all.

Group R females were characterised not only by showing typical behaviour in response to stimulation with male normal song, but also by their stridulation response to this stimulus. During the course of various behaviour experiments, female stridulation was recorded and analysed and Fig. 2 (E & F) shows an oscillogram and audiospectrogram of the song. Its general similarity to male normal song (Haskell, 1957) is obvious. Group R females would in general readily respond by stridulation to natural or recorded male normal song or imitations of it, and this response was inhibited as in the previous species by the approach of oviposition.

Three Group R females were placed in the observation cage in the centre of which was placed a smaller cage of perforated zinc in which were several males. When the males were provoked to sing by artificial stridulation, the females stridulated in reply, orientated to the small cage and moved towards it. Arriving there, some alternation of stridulation occurred, with the males moving restlessly inside the cage and the females moving up and down outside and climbing over the top. Once or twice antennal

contact was effected through the holes in the zinc. After some time the situation resolved into the males singing the normal song with occasional bursts of courtship song and moving restlessly about the inner cage; the three females sat near or on the cage, very occasionally stridulating in reply but becoming more and more unresponsive. The females were left in this situation for three days, at the end of which time the males were still singing but the females seemed not to be affected by the songs. They were distributed about the observation cage, feeding or sitting still; they were unaffected by playback of male normal song at high intensity (+70 dB.). The males were now released from the inner cage; after initial displacement had ceased, one began to sing the normal song and another responded but the females made no reply. However, the males, moving about eventually encountered the females at close quarters and at once began to sing the normal song. Two of the females responded at the fourth and fifth burst of song respectively, and then courtship and copulation proceeded in the normal manner. The third female did not stridulate, but when a male, having sung the courtship song, sprang on her she did not refuse to copulate. None of these copulations was allowed to proceed and the females were removed to an isolation cage; after 24 hours they were put back in the cage with more males in the inner cage and the experiment repeated. After three days the females were removed to an isolation cage for varying periods and then returned to the experimental cage and their reactions to male song noted. Proceeding thus, it was found that, in the three insects tested, one regained its full responsiveness to male song after approximately 13 hours in the solitary cage, another after 22 hours and the third after 27 hours.

Three more Group R females were taken and allowed to copulate fully with males; they were then put in the observation cage with males in the inner cage. They showed no response to stridulation during a 7-day observation period, and would not allow copulation when the males, on release, encountered them in the course of their random wanderings. The females, on being removed to an isolation cage and being tested by putting males in for one hour daily, regained the responsive state but after considerably longer periods than in the previous experiment, the times being 6, 8, and 12 days respectively.

The compound eyes of two Group R females were covered with black lacquer and they were placed in the observation cage with a single male. This latter was induced to sing the normal song by stimulation with artificial stridulation, and one of the females responded by orientating towards the male and stridulating. Subsequently this female moved towards the male through the grass on the floor of the cage in a reasonably direct line until she was about 5-6 cm. from him. She then seemed uncertain as to the location of the male (who, owing to a heap of grass could not see her) and repeatedly orientated in various directions while stridulating in response to the male. The latter was also moving about a little and after a short time saw the female, at once moved rapidly towards her and began the courtship song. The female did not orient towards the male, who approached her from behind, but after a short burst of courtship song the male leapt on her back and copulation proceeded normally. Substantially the same observations were made on the second blind female when, after a direct approach towards the stridulating male, the female became very uncertain in her movements when within a few centimetres of him; when the male found her, however, copulation was not refused.

Chorthippus parallelus

Typical behaviour in this species is as follows: when a male begins to sing the normal song, females within range, who are in the responsive state, orientate to the source of sound and move towards it. Generally, while pausing during movement to re-orientate, they make the female "response stridulation movements" with their hind legs. These movements produce no sound since females of this species are brachypterous; in the descriptions of behaviour which follow the term "response movements", when applied to a female, will refer to these motions of the hind femora, which appear to be identical with those of the hind femora of a male singing the normal song. When responsive females come within sight of a male, they move directly towards him and stand nearby, making response movements as a reaction to the normal song of the male. When the attention of the male is attracted to the female, he at once goes up to her, gives a short burst of courtship song and leaps on her back, copulation ensuing. It is probably more correct to regard this latter song of the male as a "shout of triumph" (Haskell, 1957).

Table II. ***C. parallelus*** **Females Group S/M/B: Reactions to Normal Song of Adult Mature Males over a Period of 35 Days Compared to Position in Oviposition Cycle. + indicates complete response to male song, including stridulation, orientation and movement; + partial (+P) indicates orientation and search but no stridulation; — indicates no response. "Ov" indicates day on which an egg pod was laid. Complete copulation (CC) indicates copulation allowed to go to its natural conclusion.**

Date	Insect no. 1	2	3	4	5
Sept. 27th	—	—	—	—	—
„ 28th	—	—	—	—	—
„ 29th	—	—	—	—	—
„ 30th	—	—	—	—	—
Oct. 1st	—	—	—	—	—
„ 2nd	—	—	—	—Ov	—
„ 3rd	—	—	—	—	—Ov
„ 4th	—	—Ov	—Ov	—	—
„ 5th	—Ov	+	+	—	—
„ 6th	—	+	+	—	—
„ 7th	*Died*	+	—	+Ov	+Ov
„ 8th		+	+Ov	+	+
„ 9th		—Ov	+	+	+
„ 10th		+	—	—Ov	+
„ 11th		—	+	+	+
„ 12th		+Ov	+Ov	+CC	—
„ 13th		+	+	—	+Ov
„ 14th		+	+	—	+
„ 15th		—	+CC	—Ov	+
„ 16th		+Ov	—	+	+
„ 17th		+	—	—	+
„ 18th		+	—	—	—
„ 19th		—	—	+	+Ov
„ 20th		+Ov	+Ov	+Ov	+
„ 21st		+	+P	+P	+
„ 22nd		No test	No test	No test	No test
„ 23rd		No test	No test	No test	No test
„ 24th		+	—	—	+
„ 25th		+	—	—	—
„ 26th		+	—	—	+Ov
„ 27th		—	*Died*	*Died*	+P
„ 28th		+Ov			+P
„ 29th		—			—
„ 30th		*Died*			—
„ 31st					*Died*

Group S/M/B, consisting of five females, was allowed to mate completely and was then returned to a cage containing adult males. During an observation period of 18 days, only one of these females allowed copulation; at the end of this period the group was removed to an isolation cage and a single adult put in for an hour every day to test their responsiveness. Table 2 summarises the reactions of each insect from September 27th, the date when the group was isolated again, until the death of each insect. The table shows in various insect the recovery of response after initial copulation, temporary blocking of the response by oviposition, inhibition of the response for a varying period by a second copulation and the disappearance of the response a few days before death.

Females of Group S/M/S recovered their responsiveness when returned to isolation in the same manner as *C. brunneus* Group S/M/S, but in *parallelus* the process took a shorter time, as Fig. 7 shows. Only seven out of the eight females in the group recovered the response, the eighth never again responding to stridulation and refusing all atteapts at copulation.

The females that recovered the response were used in experiments to determine the role of vision in stridulation behaviour. Blind females behaved in the same manner as blind females of *C. brunneus*—they moved reasonably directly towards a singing male, but became more and more uncertain in orientation the nearer they got to him. However, once a male saw a female the normal behaviour was elicited and copulation

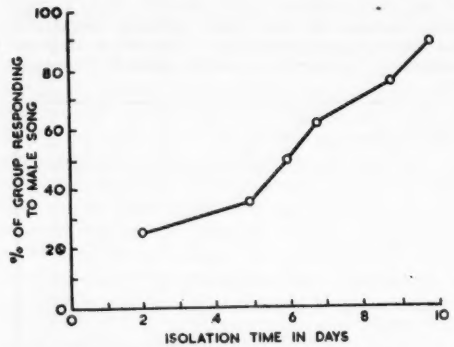

Fig. 7. Increase in positive response to song of *C. parallelus* Group S/M/S as a function of isolation time.

ensued. If the males were also blinded, however, contact was very difficult to establish and the two insects would circle round one another for as long as ten minutes before a chance contact brought them together. Under these circumstances, the females on being touched, say, by the antennae of the male, would often lash out with their hind legs and sometimes jump away, and thus the whole procedure for meeting had to begin again.

The main experiments on *C. parallelus* females were done with members of Group R. Six Group R females were placed in the observation cage, at one end of which was a small (3-inch square) cage of perforated zinc containing a single adult male, which was provoked to sing the normal song by artificial stimulation. All the females oriented towards the source of sound and began to move towards it; the track of the females was fairly straight, deviations being caused by obstacles such as clumps of grass or twigs. Four of the females now had one of their tympanal organs destroyed, two the left-hand organ and two the right-hand; after an hour these insects were returned to the cage with the intact females. When the male sang, all six insects still oriented and moved towards the source of sound, and made response movements, but the four insects with punctured tympanal organs now made a much more hesitant approach with frequent stops. It was noticeable in these females that they frequently turned half circles with their intact tympanal organ towards the source of sound, and then straightened up and moved forward. Such location procedure was more evident the closer they got to the singing males, but all six eventually located the cage. The females were again removed and both tympanal organs of all six destroyed; when, after an hour, the experiment was repeated, no response to male song was observed. No change in the manner or in the efficiency (measured by path length) of the directional response to a singing male was noted when normal Group R females had their thorax, abdomen and anal cerci smeared with vaseline, which has the effect of abolishing the responses to sound of the abdominal hair organs and sensillae on the anal cerci (Haskell, 1956a).

Fourteen fourth instar female nymphs were weighed daily and tested for response to male normal song. Table III shows the number of days after the final moult and their weights when they became responsive to male song. These fourteen adults were then kept in the solitary state and tested daily for responses to natural and artificial stridulation; they were also weighed daily and their ovipositions noted. Table IV sets out the data of this experiment and the following information may be derived from it: 58 oviposition periods were observed in this experiment; of these 52 could be described as normal in that they did not come during a period when the response to stridulation was blocked by various conditions, such as, for example, recent copulation (Insect No. 7, oviposition of Oct. 12th and 16th) or approaching death (Insect No. 1, oviposition of Nov. 12th).

Table III. *C. parallelus* Females Group R: Time of Onset of the "Responsive State"

Insect No.	Number of days between final moult and appearance of responsive state	Weight in milligrams at appearance of responsive state
1	14	165
2	12	151
3	13	159
4	16	179
5	16	170
6	16	180
7	16	176
8	13	165
9	15	176
10	18	201
11	14	176
12	14	167
13	12	158
14	17	194
	Average number of days between final moult and appearance of responsive state = 14·7	Average weight at appearance of responsive state = 172·6 mg.

Table IV. Variation of Response of *C. parallelus* Females Group R to Artificial and Natural Stridulation, with Oviposition and Age

Table IV. Variation of Response of *C. parallelus* Females Group R to Artificial and Natural Stridulation, with Oviposition and Age

Insect No.	September 27	28	29	30	1	2	3	4	5	6	7	8	9	October 10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	November 1	2	3	4	5	6	7	8	9	10	11	12	13	14
1	+ MA	+ MA	+ MA	+ MA	+ MA	+ M	+ MA OV	+ MA	+ MA	+ A	— OV	Died																																					
2		+ MA	+ MA	+ MA	—	+ M OV	+ M	+ M	+ M	—	+ M OV	+ M	+ M	—	+ MA	+ MA OV	+ MA	+ MA	+ MA	+ MA OV	+ MA	—	—	—	+ M OV	+ M	+ M	+ M	+ M	+ MA	—	+ M	— OV	—	—	—	—	—	+ MA	+ MA	+ MA	+ MA	—	+ MA OV	—	—	—	—	Died
3			+ MA	+ MA	+ MA	+ M	+ M	+ M OV	+ M	+ M	+ M OV	+ M	+ M	+ M		+ M OV	+ M	—	+ M OV	+ M	—	+ M OV	+ M	—	+ M OV	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	Died							
4			+ M	+ M	+ M	+ M	+ MA	+ M	+ M	+ M OV	+ M	+ M	—	—	+ MA OV	+ MA	+ MA	—	+ MA OV	+ MA	+ MA	+ MA	— OV	—	+ MA	—	—	—	—	+ M OV	+ M	—	+ M	—	+ M	—	—	+ M	—	—	—	—	Died					
5						+ M	—	+ M OV	—	—	Died																																							
6							+ M	+ M	+ M	+ M OV	+ M	+ M	—	+ M OV	+ M	Died																																			
7						+ M	—	+ M OV	+ M	—	+ M OV	+ M	+ M	— (see note 1)	—	—	— OV	—	—	—	— OV	—	—	—	+ M OV	+ M	+ M	+ M	+ M	+ M	—	+ M OV	+ M	—	+ M OV	+ M	—	+ M	—	—	—	—	—	—	Died						
8									+ M	+ M	+ M	+ M	—	+ M OV	+ MA	+ M	—	—	— OV	—	Died																													
9														+ M	— OV	—	+ M	—	+ MA OV	+ M	— OV	+ M	—	—	+ M OV	+ M	—	—	Died																									
10															+ M	+ M	+ M	— OV	+ M	—	+ M OV	+ M	—	+ M OV	+ M	+ M	—	+ M OV	+ M	—	—	—	Died																				
11															+ M	—	+ M OV	+ MA	—	+ MA OV	+ MA	+ MA	+ MA	—	+ M OV	+ M	+ M	+ M	+ M	+ MA	+ MA	+ M	—	+ MA OV	+ MA	+ MA	+ MA	—	+ M OV	+ M	+ M	—	—	—	Died					
12																	+ M	—	+ M OV	+ M	—	—	—	—	—	Died																									
13																		+ MA	+ MA	+ MA	+ MA	—	+ MA	+ MA OV	+ M	—	+ M OV	+ M	+ M	+ M	+ M	+ MA	+ MA	Died																		
14																			+ MA	+ MA	+ MA	+ MA	—	+ M OV	+ M	+ M	+ M	+ M	+ M		+ M OV	+ M	—	+ M OV	+ M	+ M	+ M	+ M	+ M	+ M OV	+ M	+ M	—	—	—	—	Died		

Legend: M=male song; A=artificial stimulus; +=positive reaction; —=no reaction; OV=egg pod laid. *Note* 1: This female had complete copulation at this time

Of these 52 normal ovipositions, 43 or 82 per cent. caused the blocking of the responsive state either on the day of oviposition or for 24 hours earlier. In 5 out of the 14 insects the first oviposition after the onset of responsiveness was not inhibitory to the response. The alternation between responsiveness to both natural song and artificial stridulation, and to the former only, was very irregular; one of the difficulties in this experiment was in keeping the intensity and pulse repetition frequency of the artificial stimulus, made by mouth by the observer, the same for all experiments, and the variations in response may be due to this. In 11 out of 14 insects the approach of death caused a cessation of the response between 2 and 17 days previously. In the three cases (Insect Nos. 2, 4 and 9) where two or more days of unresponsiveness appeared in the middle of responsive periods for no obvious cause, this unresponsiveness was terminated at the next oviposition.

Nine Group R females were placed in the observation cage and recordings of the normal song of the male were played back through a small 3-inch speaker in the cage. All the females orientated to the sound, made stridulation response movements and moved towards the speaker. A low-pass filter was now inserted in the circuit to produce frequency distortion of the sound, the intensity was adjusted to the same value as previously, and the experiment repeated, the females reacting as before. The experiment was again repeated, but this time the tape speed of the recorder was reduced by half, thus introducing frequency distortion and reducing the pulse repetition frequency of the stridulation by half. Under these conditions only one female responded by orientation although it made no response movements, and the remaining females gave no response at all. This experiment was repeated three times; the insertion of the low-pass filter did not affect the responses of the insects, but playback at reduced speed only elicited confused orientation reactions and no response stridulation movements. No response movements or locomotor reactions could be elicited from Group R females by any song of the male other than the normal song, nor was any response observed to natural or recorded stridulation of any of the other three species studied.

Three Group R females were exposed to natural male song, without being allowed to contact the males, for varying periods up to 48 hours; such exposure did not inhibit response with typical behaviour when males and females were put together in the observation cage.

Six Group R females were allowed to copulate; three were then taken and put into an isolation cage, the remaining three being put in the observation cage with males in a smaller inner cage. The two groups of females were tested daily for response to natural male song; the group which had been removed to an isolation cage began to recover the responsive state in six days and by the eighth day all three insects were fully responsive. The group which was kept in the observation cage showed no reactions to male song and actively refused copulation. At the end of eight days, when the isolated group had all recovered responsiveness, the second group of females was also isolated and regained their responsiveness in 4, 6 and 9 days respectively.

Four groups of six insects each of 3rd instar female nymphs of *C. parallelus* were kept isolated and subjected to playback of various sounds for an hour three times daily from the date of capture until moulting to adults, and thereafter until their weight curve showed them to be mature. The sounds used as stimuli for the various groups were:

Group 1. Normal song of a male *O. viridulus*.

Group 2. Imitation by mouth of normal song of male *C. parallelus*.

Group 3. Recorded normal song of male *C. parallelus*, played at slow speed.

Group 4. Recorded normal song of male *C. parallelus* played at correct speed.

After the insects in the groups had all been allowed to oviposit once, they were tested daily for reactions to the sounds to which they had been subjected during breeding. The only groups to show any responses were Groups 2 and 4 and these responded with typical behaviour to their group stimulus; Groups 1 and 3 did not show any response to the sounds to which they had been subjected, but gave typical behaviour responses when stimulated with natural normal male song of *C. parallelus*.

During the experiments described above to determine the role of the tympanal organs in typical behaviour, on one occasion a response was obtained from an insect with both tympanal organs destroyed. In view of the capabilities of the abdominal hair sensillae of the four species in responding to airborne sounds (Haskell, 1956 a & b) experiments were made to ascertain if these sense organs were capable of mediating the typical behaviour in responsive females. Three Group R females had both

tympanal organs destroyed by the method previously described; 12 hours after the operation they were tested against natural male normal song and gave no responses. They were also tested against playback of the same song at various intensities but gave no responses. Similar tests 48 hours after operation produced no reaction, but after 72 hours two out of the three females made response movements on playback of the male normal song at a high intensity (80 dB at 30 cm. from the insect). The response movements were identical with those called forth by stridulation when the tympanal organs were intact, but, although the two responding females moved about, no directional response was seen. After a further 24 hours, the remaining female also made response movements but again only to playback of high intensity. It was found that the minimum intensity for excitation was of the order of 65 dB at 30 cm. from the insect. The reaction to playback was quite quick but no directional response was ever observed; the response was blocked by oviposition as in normal females. Smearing the thorax and abdomen with vaseline caused the response to disappear. In all three insects dissection after death showed the tympanal organs to have been destroyed. One further interesting observation was made with one of these females which had had both tympanal organs destroyed and also the thorax and abdomen smeared with vaseline. No response to playback of male song at high intensity was obtained until by accident the 3-inch speaker through which the stimulus was being given was placed on the floor of the cage about 15 cm. from the test insect. Playback then elicited the stridulation response movements from the female, but no locomotor or orientation behaviour accompanied this.

Discussion

It is evident from the experiments described above that behaviour associated with stridulation in the females of the present four species conforms to a common pattern, with minor variations from species to species, at least in so far as the responses to male normal and courtship song is concerned. This common pattern has been called "typical behaviour" and the experimental evidence throws light on the onset of this state and its inhibition at various times during the life of the female. This typical behaviour can rarely be seen in nature and can seldom be demonstrated in mature females taken from the field. Obviously the readiness of a female to react to male song varies and only in a certain physiological state will it respond with full typical behaviour; this physiological state has been termed for obvious reasons the "responsive state". Regen (1923) found that only adult but unmated females of *Gryllus campestris* responded to the male song and Baier (1930) confirmed this for other Orthoptera. In the present four species it has been shown that the onset of the responsive state appears to correspond with the maturation of the ovaries. Females kept isolated from the third instar did not become responsive as soon as they moulted to adults, but at varying times after this. The time after moulting when the responsive state appeared was, as an average, 12.8 days for *brunneus* and 14.7 days for *parallelus* and the mean weights at these times were 204.8 mg. and 172.6 mg. respectively. Richards & Waloff (1954) in their study of maturation in these species, give the average time for the attainment of maturity in the two species as 14-15 days and as approximations of the mean mature weights 188.7 mg. for *brunneus* and 160.3 mg. for *parallelus*. This figure will vary from year to year and thus a close agreement is not to be expected, but the present figures clearly support the conclusion that the responsive state appears at maturation, probably when the first egg in the first ovariole is ripe. This agrees with the findings of Renner (1952) for the Acridid *Euthystira brachyptera*.

The inhibition of the responsive state by oviposition was clearly demonstrated in all species except *S. lineatus*, for which oviposition cycles were not obtained. The evidence available suggests that the response to song is inhibited for a varying period before the act of oviposition, ranging from 24 down to about 10 hours, and is recovered after oviposition within one or two hours at the most. Renner (1952) working with *Euthystira brachyptera* related the onset of inhibition to the actual movement of eggs in the ovaries and found that the inhibition period begins as soon as the eggs move from the ovarioles to the lateral oviducts. In the experiments with *C. parallelus* it was found that in 35 per cent. of cases the first oviposition after the onset of responsiveness caused no inhibition, and that when periods of inhibition appeared for unknown reasons in the middle of a period of responsiveness, this inhibition was generally terminated after the next following oviposition. It seems possible that this inhibition

may be due to some eggs remaining in the oviducts and not being fully expelled at one oviposition and is then terminated at the following oviposition when all eggs are fully expelled.

The approach of death also produced inhibition of response, even though in many cases oviposition occurred normally within one or two days of death. This again may be due to egg rudiments remaining in the oviducts or perhaps to some change in metabolism caused by the moribund state of the insect. Richards & Waloff (1954) point out in this connection that physiological old age in these grasshoppers is accompanied not by a reduction in the number of egg rudiments but by failure to produce yolk for the eggs to mature. This may be caused by some failure of metabolism which contributes to the loss of responsiveness at the approach of death.

The evidence from all four species clearly shows that the responsive state is terminated by copulation; once again this is in agreement with Renner's findings on *Euthystira brachyptera*. He also states that the response is inhibited until after several ovipositions and argues that the state of the receptaculum seminis is responsible for the control of this period. The effect may be mechanical, due to the filling of the organ with sperm, or hormonal. However, the process of inhibition and recovery in the present grasshoppers seems to be more complex than this. They regained the responsive state after copulation in a period of time which varied with the species; during this time oviposition occurred but was not sufficient in itself to cause recovery of the responsive state, which was only restored when the females which had mated were isolated from males. The continuance of the inhibition of the responsive state in females allowed to mate once and then kept in the company of males may have been due to a number of factors, such as continual attempts by males to mate, the sight, smell or song of the males. However, the experiments with *C. brunneus* and *C. parallelus* females strongly suggest that the inhibition lasts as long as the females hear the sound of male normal song. Females kept under such conditions rarely recovered the responsive state and this fact explains the very few copulations noted in the breeding cages of the four species, whereas females in non-breeding groups were far readier to copulate. The exposure to male song must however be continuous or go on for long periods, since in experiments where females were recovering the responsive state in isolation, they were tested for this by placing males in the cage for an hour daily and this short exposure to male song did not apparently retard the recovery appreciably. In view of the work of Norris (1954) it would be as well to emphasise however that the present experiments do not preclude the possibility that the sight or smell of males may be factors involved in continuing inhibition.

Copulation was only effective in inhibiting the responsive state when allowed to go to completion or at least to the stage when the spermatophore was passed into the female. Junction of the genitalia for periods up to 30 minutes, without passage of the spermatophore, was ineffective in inhibiting responsiveness. Although it was possible to suppress part of the typical behaviour of *C. brunneus* females by exposing them, when in the responsive state, for long periods to male normal song, they still responded to male courtship song and allowed copulation, while similar experiments with *parallelus* females produced no inhibition at all. Thus it can be assumed that only complete copulation will result in inhibition in the present species, and this inhibition may be considerably prolonged if the female is kept within the sound of male normal song. Inhibition cannot apparently be prolonged indefinitely, however, because females kept in breeding cages did sometimes allow copulation, although they did not exhibit typical behaviour at all, but seemed rather to be in a passive state, when prolonged courtship induced them finally to allow copulation. Renner (1952) states that such a passive state characterises females of *E. brachyptera* after copulation, but this is not so in the great majority of observations on the present species, when the female in the post-copulation period shows the normal defence and rejection behaviour towards males.

It seems likely that the inhibition of responsiveness by oviposition and copulation involves alterations in the higher nervous centres, although the intermediate mechanisms could be chemical. Inhibition before oviposition may be connected with the hormonal changes associated with this act (Weed Pfeiffer, 1939, 1945); however, no direct evidence is yet available on the stimulus which causes eggs to enter the oviducts prior to laying, which is, according to Renner (1952), the specific act causing inhibition of the responsive state, although Iwanoff & Mestscherskaja (1935) claim that a hormone originating in the corpus luteum influences the ovarial cycle. Certainly, inhibition

is not peripheral, as was shown by Haskell (1956 a b), since electrophysiological experiments on tympanal nerves show the same responses to song whether the females used were virgins, about to oviposit or had just copulated.

The present work shows in correct perspective the full significance of female stridulation; although this has been noted by many authors, it has generally been dismissed as of little significance. However, Ragge (1955 a) remarks of female striduation in Acrididae that "it is probable that the females only stridulate during a certain phase of their sexual cycle, the infrequent observations of it suggesting that this phase is normally short-lived. As female stridulation seems to be much more prevalent in the absence of males, it is likely that the presence of the latter is responsible for inhibition of stridulation, which would be effected almost certainly by copulation. The conclusion . . . . then is that female stridulation occurs when the female is in a suitable state for copulation, and that it terminates, at least temporarily, when the latter takes place. In the case of *C. parallelus*, the commencement of female stridulation after the removal of most of the males from the cage suggests that the physiological state relating to its occurrence may reappear in the absence of repeated copulation." All these deductions are upheld by the present work; the paucity of observations on female stridulation in previous work also supports the conclusion that females taken in the field only rarely are in the responsive state.

The above observations go some way towards clearing up the variable results achieved by many workers in relation to behaviour and song in various Orthoptera. For example, Broughton (1952) obtained on one occasion only responses to playback of male normal song from females of *C. brunneus*; it seems probable that the responding females had just entered the responsive phase. On the other hand, Busnel & Busnel (1955) obtained positive locomotor responses from four out of ten females of *Oecanthus pellucens* to playback of male song, and all these females had been chosen as being in a state ready to copulate with males. However, the females after being chosen were kept in a cage for two days to settle down and two days is sufficient time for the responsive state to be inhibited by hormonal or other action, and, in fact, two of the non-responsive females were seen to be ovipositing during the experiment. It is clear from the present work that it is essential in using insects for playback or behaviour experiments connected with stridulation that the whole of their sexual and ovipositional history should be known in order to be able to assess with any accuracy the likelihood of their being in the responsive state.

The experiments described above allow us to assess some of the sensory modalities involved in stridulation behaviour. It is clear from the experiments on *C. brunneus* and *C. parallelus* females that the tympanal organs act as the main initiators and directors of the behaviour. That they also are used to guide the insect to the source of sound was demonstrated by the behaviour of insects with only one functional organ. However, the behaviour of blinded females shows that as the female approaches the male, visual responses come more and more to the fore, and this observation is in agreement with the fact that the directional efficiency of the tympanal organs will fall off as the female approaches nearer and nearer to the source of sound (Pumphrey, 1940). This reliance on vision in the final meeting of the sexes is underlined by the experiments in which both males and females were blinded, when they found one another by chance after much aimless wandering. This use of two sensory modalities and the switching to vision at the end of the female's approach would result in the greatest efficiency in the typical long grass habitats of these species, where acoustic range is certain to be greater than visual range at the outset, but where vision can replace inefficient sound location at short range.

It seems unlikely, for reasons given elsewhere (Haskell, 1956 a & b), that the hair sensillae on the thorax and abdomen of the present species play any part in sound reception in the field. The responses noted during the present work by insects with their tympanal organs destroyed were only elicited by signals of very high intensity (65 dB) and, as has been shown by Haskell (1955a), intensities of this order only occur in field conditions within a few centimetres of the emitting insect. What was interesting about the present observation was that the stimulus, received by the hair sensillae, elicited from the female the same stridulation response movements as given to stimuli received via the tympanal organs, and the response appeared long after the destruction of the latter. In another experiment, when the responses of the abdominal hair sensillae had also been

abolished by smearing thorax and abdomen with vaseline, stridulation response movements were elicited from a female *parallelus* apparently in response to stimuli transmitted via the substrate and presumably detected by the subgenual organs in the legs. The production of stridulation response movements following stimulation of either the hair sensillae or the subgenual organs seems surprising, since in neither case does it appear likely that discharges in the afferent fibres of those organs would reflect any characteristic feature of the stridulation (such as pulse repetition frequency), although as experiment has shown (Haskell, 1956b) this may be possible in abdominal hair sensillae in certain special cases of which *C. parallelus* is one. There is one aspect of behaviour in which these organs may play a part, however, and that is during courtship and mating; many Acridid courtship songs (e.g. *C. jucundus*) are characterised by a high sound intensity and at the close ranges involved in courtship, the intensity may be sufficient to stimulate the abdominal hair sensillae. Haskell (1955b) has also shown that stridulation in certain grasshoppers produces vibrations of the substrate of such magnitude that they can be detected by the subgenual organs at distances of the order of 15-20 cm. Thus again during courtship these organs may come into play, but much further investigation is needed in order to assess these possibilities.

The responses of females with intact tympanal organs to distorted playback of male normal song were the same as those reported for males (Haskell, 1957) and are consonant with the hypothesis that the principal feature by which specific recognition of songs is accomplished amongst these insects is the pulse repetition frequency of the sounds (Haskell, 1956 a & b). Whatever this discrimination mechanism is and however it operates, it is apparently innate, since conditioning of *C. parallelus* nymphs to various sounds during rearing produced no enhanced responses to these sounds in the adult, nor was the stridulation behaviour of the mature insects altered in any way. In view of some of the evidence on this aspect of the behaviour, notably that of Regen (1926) relative to newly emerged adults of the Tettigoniid *Thamnotrizon*, this last result may only cautiously be accepted and it may prove that conditioning occurs earlier than in the 3rd instar in *C. parallelus*. Unfortunately no data are available as to the earliest instar during which the tympanal organs are functional and consequently at which conditioning may occur.

The majority of the evidence presented here and in the previous paper (Haskell, 1957) points to the conclusion that the mechanism of song discrimination in the present species is innate; such a mechanism, which discriminates between intra-specific stridulation and all other sounds on the basis of pulse repetition rates, would insure against the possibility of a newly-moulted insect learning an incorrect song pattern (a possibility which might occur in these grasshoppers which live side by side in the same habitat if the mechanism was entirely learnt). The importance of such a mechanism is clear when it is realised that courtship can only lead to successful copulation in the present species when stridulation is used; males of *C. brunneus* with tegmina removed, incapable of stridulation, were invariably rejected by females, even those in the responsive state, and no response to extra-specific stridulation was obtained from males or females. It is equally important for both males and females in any one species to respond to the "correct" songs and discriminate against the "incorrect" ones, and this suggests that the mechanism in both sexes will be similar. Now it is clear that the stridulation movements themselves, at least of males, are governed by a true instinct, an inherited and adapted system of co-ordination. In females, at least of the species here studied, the stridulation movements of the hind femora greatly resemble those of the male of the species, and in some cases (notably *O. viridulus*) the sound produced is very similar. It is therefore perhaps permissible to postulate that the same instinctive motor pattern of stridulation movements is common to both males and females, but in the latter is only evoked when the female is in a particular physiological condition.

In both sexes, full typical behaviour in response to normal song of the male consists of three phases: stridulation, orientation and locomotion. In the field this behaviour is either partly suppressed, as in the male, or wholly suppressed, as is generally the case in the female, but in both sexes will re-appear after a period of isolation. In the absence of members of the opposite sex, operation of the first phase of behaviour leads to group singing, as for example in *O. viridulus* males or as in *C. brunneus* females (Haskell, unpublished results). When in the responsive state, the full working out of the typical behaviour pattern by either males or females leads to inhibition of that state. The system in females is more complicated because it is affected by the reproductive activity

of the insects, but there seems to be enough evidence to make it probable that stridulation behaviour in both sexes of all four species at present studied is mediated by a similar mechanism.

Finally, it is possible by using the observations discussed above to form a reasonable picture of events in the field concerned with mating in the present species. These insects tend to live in "colonies" (Richards & Waloff, 1954) characterised by a relatively high population density within a fairly small area. After moulting to an adult, a female will become responsive at maturation. When this occurs she will display typical behaviour in full the first time she hears male normal song; on reaching the male she will mate. She may also meet in the course of her movements another male, or may, while response, accidentally meet a male; in either event the male, on visual stimulus, will sing the courtsthip song and copulation will ensue. The female now loses the responsive state and goes about the process of repeated oviposition without responding to further male song. After a period of time (not determined) she may recover the responsive state and the process will be repeated. Alternatively, if she wanders away from the main colony the responsive state will return in a time dependent on the species and she will then be re-attracted back to groups of singing males of her own species as soon as she comes within acoustic range and again the pattern is re-established. Since females move relatively little in the field (Richards & Waloff, 1954), it seems likely that the great majority of females having once copulated, always stay within range of one male or another and will rarely regain the responsive state, or at least only after long periods. This general picture is consonant with what is known of the general biology and ecology of the present species as described by Richards & Waloff (1954).

Summary

1. The stridulation of females and their behaviour in relation to males was studied comparatively in the following species of Truxalinae: *Stenobothrus lineatus* (Panzer); *Omocestus viridulus* (Linnaeus); *Chorthippus parallelus* (Zetterstedt); and *Chorthippus brunneus* (Thunberg) (=*C. bicolor* Charp.).

2. Descriptions of the "typical behaviour" of females in response to normal song are given. This behaviour is similar in all species and consists of three phases: response stridulation, orientation towards and locomotion to the male. Arrived near the male, the female stridulates in response to male song; the male, on noticing the female, sings the courtship song, engages the genitalia and copulation ensues. Females showing such typical behaviour are said to be in the "responsive state".

3. This responsive state in females of the four species appears at maturation, is inhibited for periods up to 24 hours prior to oviposition, is regained shortly afterwards and is lost some days prior to death. Complete copulation involving the transfer of a spermatophore also inhibits the responsive state in the females; if the latter are isolated after copulation, they regain their responsiveness in a period of from 6-20 days dependent on the species. This recovery is delayed or prevented if the females are kept after copulation with males or within the sound of male normal song.

4. The responsive state is characterised in most females of all four species by the emission of stridulation in response to male normal song. In all cases, the movements of the hind femora of a female emitting this stridulation are very similar to those of a male of the same species singing the normal song. In the case of *S. lineatus*, *O. viridulus* and *C. brunneus*, audible sounds are emitted by the females, which in the case of the latter two species show marked affinity to male normal song. Physical analyses of these sounds are presented. Females of *C. parallelus*, being brachypterous, emit no sound while making stridulation movements of the hind femora.

5. It is postulated that the discrimination mechanism responsible for distinguishing between various specific songs is closely linked to the inherited motor mechanism which causes typical stridulation in both sexes. It is further suggested that the basic behaviour reactions of males and females to male normal song are the same, consisting of stridulation response movements, orientation and locomotion towards the male. Normally in the field, the last two phases are suppressed in males, the whole sequence in females. Isolation restores full typical behaviour in both males and females and, in the latter, stridulation is always an indicator of the return of the responsive state.

6. The observations are used to construct a possible picture of events in the field concerned with courtship and mating in the present species.

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A FAILURE TO FIND SOCIAL FACILITATION OF AUDIOGENIC SEIZURES IN THE RAT

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Current interest in audiogenic seizures centres about the influence of complex variables on the incidence and severity of the attacks. For example, several investigators have been concerned with the relationship between emotional factors and susceptibility (Martin & Hall, 1941; Lindzey, 1951; Griffiths, 1953), and others with the influence of early experience on seizure behaviour (Hall & Whiteman, 1951; Bingham & Griffiths, 1952; Griffiths & Stringer, 1952; Bevan, Grodsky & Bostelmann, 1956). Despite this interest there is still considerable disagreement as to the relationship of emotionality (innate or acquired) to convulsions. In addition to emotional factors and early experience, several workers in this area have expressed the personal belief that "one animal sets the other animal off", if more than one animal is tested at a time. Anderson (1939), however, reports that the presence of a second animal did not modify the emotional behaviour of rats, as measured by counting and weighing of the faeces. Hall & Margin (1940, p. 209) likewise claim that testing as many as four rats at one time has no apparent effect on seizure behaviour, but they present no data to support this claim. Finger (1944), on the other hand, says that ". . . the noisy reactions of one animal will reinforce the clonic spasms of another . . . To the extent that such auditory stimulation may be regarded as 'social,' it is legitimate to state that the behaviour pattern can be altered by social or group factors (p. 422)."

The present study was undertaken to provide systematic observations of seizure behaviour under social and non-social (isolated) conditions.

Method

Sixteen albino rats derived from Wistar stock were housed together in pairs. There were 5 pairs of males and 3 pairs of females. Testing was begun when the animals were 44 days old, and had been caged together for a week. The test procedure consisted of placing the animals singly or in pairs in a metal tub enclosed in a sound-resistant box, and exposing them to two minutes of auditory stimulation provided by a 4-inch doorbell. A fuller description of the test procedure and apparatus is presented in Bevan & Hunt (1953).

The animals were tested every other day for 20 days. For half of the animals the initial test was with its cage mate (social condition), whereas the other half of the animals were tested initially alone (isolated condition). Thereafter the conditions were alternated on subsequent test days. At the termination of the experiment we were thus able to obtain for each animal data representing his behaviour when his cage mate was present (5 tests), and when he was isolated during the test period (5 tests). Data was collected as to the severity of the attacks, latency of the running and convulsive phases, and the duration of the running and convulsive phases of the attack.

Results and Conclusion

Only four epileptoid convulsions were observed in 160 tests; two in the social condition, and two in the isolated condition. Sixty-seven running attacks consisting of one or more bursts of violent running and circling were observed; thirty-three in the social condition, and thirty-four in the isolated condition. Due to the limited number of convulsions observed, the severity of the attacks under the two conditions was not analysed. Since each animal served as his own control, the analysis of the data consisted of tests of the significance of the differences under the two conditions of the experiment (Walker & Lev, 1953, p. 153). The results were as follows. The mean relative frequency of attacks under the isolated condition=42.50 per cent., under the social condition=41.25 per cent., $t=0.18$, $p>0.80$; the average latency of the first running attack per test under the isolated condition=27.50 sec., under the social condition=28.16 sec., $t=0.82$, $p>0.40$; and the mean duration of the total attack (running plus convulsion) per test under the isolated condition=61.45 sec., under the social condition =62.94 sec., $t=1.40$, $p>0.10$. The latency and duration averages are based only on tests during

which a response occurred. They were transformed to logarithmic values for statistical evaluation.

No instances of fighting or other clear-cut social interactions were observed at any time during the tests.

None of the average differences described above approach statistical significance. Therefore, it appears that the presence of the cage mate exerts no influence on susceptibility to audiogenic seizures. The present data also tend to support the general position that the attack, when it occurs, is not a social phenomenon in the usual sense, and that the psychological variables that are important are those that relate exclusively to the individual subject. In further investigations it is worth considering that these individual variables may effect more the precipitation of the attack, less the course of the convulsion itself.

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REVERSAL OF LEARNED RESPONSES IN *Octopus vulgaris* LAMARCK

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Introduction

The eyes and nervous system of *Octopus* are so organised that any object moving in the visual field may be attacked. The animal leaves its home, swims or walks to the moving object and seizes it with its arms (Boycott, 1954). If the situation is an unfamiliar one or beyond a certain size the probability of attack is not high and attacks are made only after rather long delay. If such attacks result in the acquisition of food the probability of attack rapidly rises, but falls if the attack is followed by a shock (Young, 1956). Presumably most octopuses attack and feed on crabs in the sea and they quickly come to do so in the laboratory. If they are given shocks when they attack a crab they will learn not to come out to attack at subsequent presentations (Boycott & Young, 1955 b). Such a memory preventing attacks on crabs is transient however; if it is not reinforced by further shocks the octopus will sooner or later again come out to attack when a crab is shown.

A memory may be defined as a set of arrangements within the nervous system that stores a representation of a selection of signals arising from a given set of events. The effect of the stored representation of the situation is to give the nervous system the capacity to make responses that are in general biologically correct, that is, tend to promote the survival of the animal. The existence of a memory representing a given set of events is thus known by the fact that the behaviour of the animal when certain events recur differs from the behaviour before their occurrence (Boycott & Young, 1955 a). In most octopuses there is present a memory that ensures that signals received from a crab produce an attack. This memory is firmly established within the nervous system, but if shocks are given when crabs are attacked a memory preventing such attacks is set up. This soon fades however and the attacks begin again. There are no data to show whether after repeated shocks over a long period, the memory promoting attack could ultimately be erased. Experiments with such "natural" situations would need to be prolonged and might prove inconclusive. We have, therefore, preferred to study the reversal of responses to artificial figures to which the animal has been trained since introduction into the laboratory. Such experiments are always open to difficulties, produced by the fact that we do not know how far the attributes of the "new" experimental situations may correspond to those of situations that the animal has already encountered in the sea.

The vertical lobe system has been shown to be involved in the setting up and maintenance of memories by *Octopus* (Boycott & Young, 1955a & b, 1956). We have attempted in the present investigation to find what part it plays in allowing reversal of learned responses. During some of the reversal trials the octopuses showed signs of the sort of behaviour shown in conflict situations by other animals (p. 7).

Methods

Octopuses were trained singly in rectangular tanks, at one end of which they made a home (Boycott, 1954; Boycott & Young, 1957). After isolation in a tank each octopus was first shown crabs at the end away from the home until it attacked these regularly, and with a delay of only a few seconds. Training was then begun, by showing a single black or white plastic figure 3 mm. thick at each trial. The figures were attached to a transparent plastic rod 6 mm. in diameter and were moved gently up and down about three times a second. If attacks were made on one figure (the "positive") food was given (a crab). If there was no attack on this figure within 15 sec. food was introduced near to it on a black thread. If there was no attack within a further 15 sec. both figure and food were withdrawn.

If the other ("negative") figure was attacked a 6-8 volt shock was given by introducing a rod carrying a pair of electrodes connected to an A.C. transformer. The octopus retreated home after a shock, but the figure was kept in the tank

for a total of 30 sec. and further shocks given on the rare occasions when there was more than one attack. If there was no attack within 30 sec. the animal was considered to have made a "correct" response to the negative figure.

Trials were given in pairs, positive and negative, separated by about half an hour. The period between pairs was at least two hours. Four pairs were usually given each day in the order: + —, — +, + —, — +.

In the presentation of the results the average number of attacks on each figure per ten trials is given. This system has many advantages, but it ignores the fact that the intervals between trials are not constant, particularly on account of the intervening night periods of about twelve hours. When the octopus had reached a suitable criterion of learning three variations of the procedure were made:

(1) Attacks on the previously positive figure were rewarded with a shock, as well as those on the negative figure. In this case food was given at the end of the day.

(2) Attacks on the previously negative figure were rewarded with a crab, those on the positive figure with shocks.

(3) Attacks on either figure were rewarded with a crab.

Methods for anaesthesia, operation and assessment of the amount of tissue removed were as in Boycott & Young (1955a).

Results

Octopus JCI was trained to attack a white circle of 6 cm. diameter but not to attack a black one of the same size (Fig. 1). After 40 trials with each figure, when its performance was nearly perfect, shocks were given when either the white or the black circle was attacked. Seven attacks were made at the white circle in the next twenty trials, which may be compared with the three shocks that were needed at the beginning of the experiment to set up a memory preventing attack on the black circle. After the fifty-sixth trial food was given when the previously negative black circle was attacked or fifteen seconds after presentation of the figure if there was no attack. The octopus then came out and took the crab, but this was of course recorded as "no attack." A memory producing attack on this figure was then slowly set up, there being only seven attacks prior to giving the crab in the first twenty trials, compared with fifteen attacks made at the white circle in the first twenty trials at the beginning of the experiment. However there was steady improvement and ultimately a nearly perfect performance, though even after forty trials there was still some tendency not to attack the new positive figure (black circle).

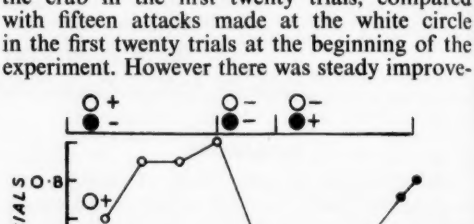

Fig. 1. Reversal of training to black and white circles 6 cm. diameter. The animal was first trained to attack the white but not the black circle. Then after the 40th trial shocks were given when the white circle was attacked. From the 56th trial food was given following attacks on the black circle or after 15 seconds if there was no attack. Ordinates show proportion of correct responses in the previous ten (or five) trials.

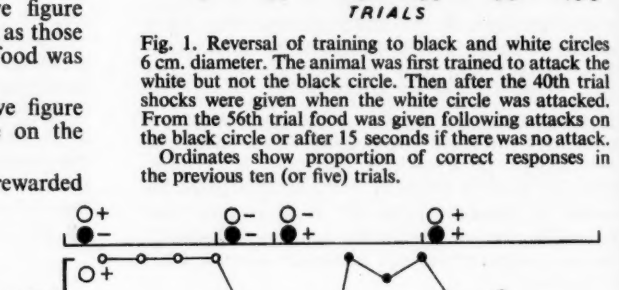

Fig. 2. Reversal of training followed by giving food with both figures. The animal was first trained as in Fig. 1. From the 40th trial shocks were given when either circle was attacked. From the 55th trial food was given after presentation of the black but not the white circle. From the 95th trial food was given following attacks on either figure or 15 seconds after presentation if there was no attack.

A similar reversal experiment with 6 cm. black and white circles is shown in Fig. 2 (JBX). When the new responses were fully established the experiment was made, from the ninety-

fifth trial onwards, of giving a crab when *either* of the figures was attacked or after fifteen seconds if there was no attack. This at first had the effect of gradually increasing the number of attacks on the negative figure. Then, unexpectedly, both positive and previously negative figures came to be treated as negative figures! After twenty trials both figures were attacked only on about half the occasions. Thereafter the number of attacks on both of them fell off until few or none were made. During the first two variations of the procedure no cautious behaviour was shown (p. 7). When both figures were rewarded, however, attacks on the crab with the former negative figure were cautious. Instead of this caution disappearing as the animal began more frequently to attack the formerly negative figure, it became exaggerated. The animal attacked the figure cautiously but now jumped back home as the crab was put in and frequently would not take it unless it was put near the home. This behaviour was transferred to the attacks on the black circle and then to the crab associated with it. Finally the octopus would not attack either figure and even sometimes would not take the crab whichever figure it was presented with. From being an octopus that showed attention to the experimenter by coming to the surface of the water whenever his head appeared above the level of the tank (Boycott, 1954), it became very withdrawn into its home.

A similar sequence of events was seen in other animals in which food was given when either figure was attacked. For example in Figs.3 and 4, with rectangles shown vertically and horizontally, or with circles of diameter3 and 6 cm. A possible interpretation of this curious effect may be that introducing the crab into *both* situations provides them with a common set of attributes. The effect of the shock, previously linked to one set of attributes (say white circle in Fig. 2), now also becomes attached to the other figure as well. At the end of the experiment of Fig. 2 the white figure was put into the tank at the *same time* as a crab for five trials, attacks being made in each trial. Further tests with the white circle alone then

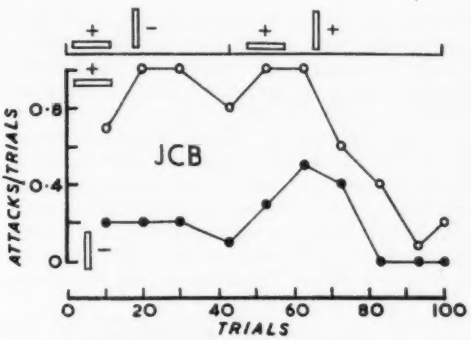

Fig. 3. Similar experiment to Fig. 2, using white rectangles 10 × 2 cm. shown horizontally (positive) and vertically (negative). After such training for 43 trials food was given for attacks on either figure or 15 seconds after showing.

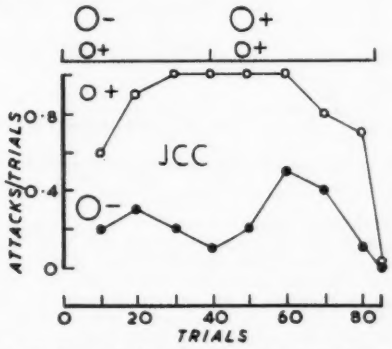

Fig. 4. Similar experiment to Fig. 3, using white circles of 6 cm. and 3 cm. diameter.

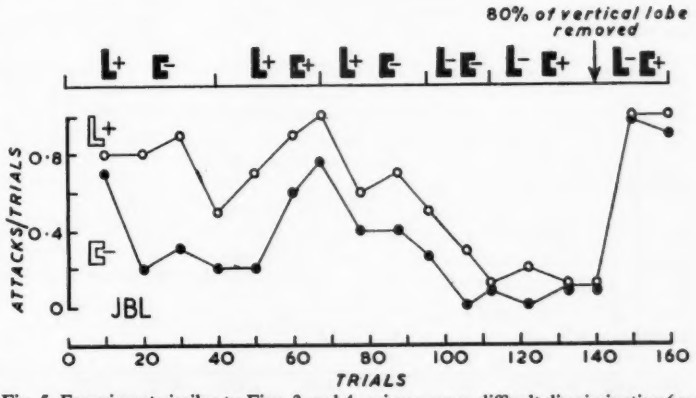

Fig. 5. Experiment similar to Figs. 3 and 4, using a more difficult discrimination (see page 48). After the 140th trial 80 per cent. of the vertical lobe was removed. For the next twenty paired trials the octopus attacked both figures equally frequently.

showed that it was now readily attacked, and some attacks were also made at the black figure. Clearly the association of both figures with shock depended upon the continual reinforcement involved in presenting each figure *alone* for 15 secs. before giving the animal a reward. When one of the figures was presented *with* a crab a memory promoting attack was rapidly built up.

In Fig. 5 (JBL) is shown a comparable experiment with two figures similar in area and length of outline, but differing in the distribution of these, i.e. in shape. These figures are discriminated at a low level of accuracy (Boycott & Young, 1956, 1957). In this case feeding after the previously "negative" figure had been shown had the effect of increasing the number of attacks on both figures (after an initial decline in number of attacks on the positive figure). Presumably, because the figures were so similar, no distinct memory preventing attack on one of them had been established. The effect of feeding after both figures was therefore to establish a common memory to attack. This was confirmed by again giving shocks (after the seventieth trial), when there were attacks on one of the figures. Immediately there was a decline in the attacks on *both* figures though there were still slightly more attacks on the positive than the negative one. Attacks on both figures became very infrequent and there was no immediate increase in the number of attacks when food was again given with one of them. However at the end of the experiment 80 per cent. of the vertical lobe was removed and the animal then came out to attack on nearly every occasion. The common memory preventing attack was, therefore, in this case, dependent on that lobe.

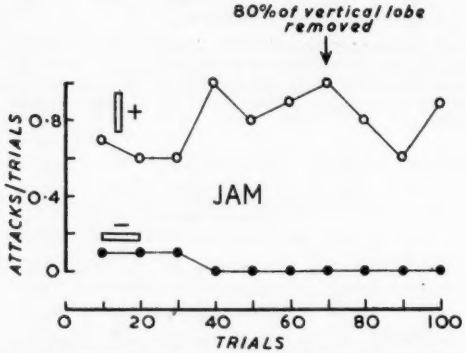

Fig. 6a. Octopus trained to attack a 10 × 2 cm. white rectangle shown vertically (positive) and horizontally (negative). After the 70th trial 80 per cent. of the vertical lobe was removed and there was a decrease in the accuracy of response to the figures. Between the 100th and 140th trial other experiments were made, not relevant here. The animal was then shown, Fig. 6b, still to be making the original discrimination with some degree of accuracy. After trial 170 it was tested for its ability to alter its reactions to the rectangles under varying conditions of reward and punishment (see text). After the 290th trial it was shown still to be attacking crabs regularly.

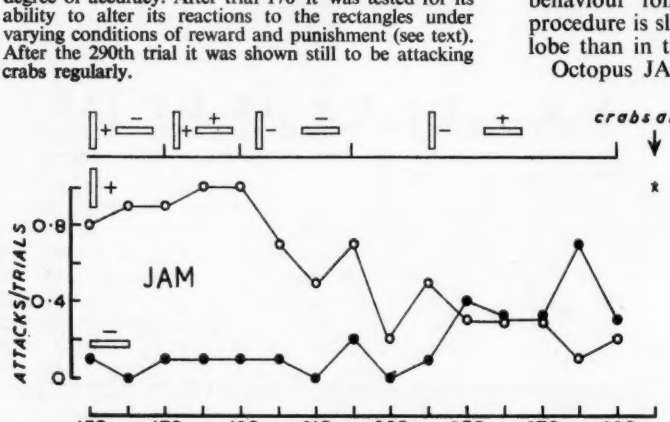

Fig. 6b

Effect of Vertical Lobe Removal on Reversal of Learned Responses

The vertical lobe is concerned with the setting up and retention both of memories that promote and memories that prevent attack (Boycott & Young, 1955a & 1957). Experiments in the present series suggest that reversal of behaviour following changes in the training procedure is slower after removal of part of this lobe than in the normal animal.

Octopus JAM (Fig. 6a) was first trained to attack a vertical but not a horizontal rectangle and 80 per cent. of the vertical lobe was then removed. The discrimination continued to be performed, approximately as before operation, though perhaps with some reduction in accuracy (Boycott & Young, 1956, 1957). After fifty trials concerned with another experiment reasonably accurate responses to the two rectangles were still being made (Fig. 6b). From the 170th trial onwards crabs were given not only with

the vertical rectangle, but also after attacks on the horizontal rectangle or fifteen seconds later if there was no attack. This did not lead to any increase in attacks on the (negative) horizontal rectangle, nor to any decrease in attacks on the positive figure, such as was seen in the normal animals of Figs. 2, 3, 4.

After the 190th trial shocks were given when either figure was attacked and there was some falling off in attacks on the previously positive figure; a falling off perhaps not as rapid as in Figs. 1 and 2. Even after thirty trials in this way the vertical rectangle was still attacked more often than the horizontal rectangle. From the 220th trial onwards food was given with the horizontal, shocks for attacks on the vertical rectangle. Performance remained very irregular, the octopus seldom coming out when either figure was shown, and attacking them about equally (cf. Figs. 1 and 2). This result is important because it shows that the effect of removal of the vertical lobe is not always to produce a state of affairs in which all figures are attacked. In this octopus, as a result of the long series of earlier trials, no memories ensuring or preventing attacks on either figure remained or could be established. As a result both figures were attacked with a frequency about that to be expected from an octopus newly brought into the aquarium (Young, 1956).

From the 290th-300th trial crabs were offered alone and the octopus attacked them on every occasion, showing that the previous failure to attack was not due to any lack, except that of a neural representation ensuring that the attributes of either of the artificial figures produced an attack. With only 20 per cent. of the vertical lobe remaining no memories could be set up ensuring that the artificial figures produced attacks.

In Octopus JCM (Fig. 7), after removal of only 40 per cent. of the vertical lobe, the animal was trained to attack a white but not a black circle. When food was given with the negative as well as the positive figure attacks on both fell off, as in a normal animal.

In Octopus JCG (Fig. 8), from which 60 per cent. of the vertical lobe had been removed before training, discrimination between vertical and horizontal rectangles was established, though with a lower accuracy of performance than in a normal octopus (Boycott & Young, 1957). Shocks were then given following attacks on the positive as well as on the negative figure, the animal being fed with crabs at the

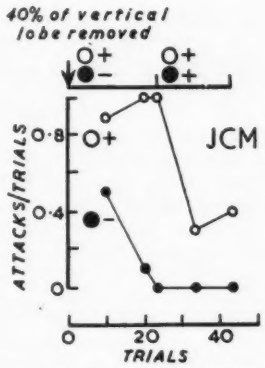

Fig. 7. Octopus with 40 per cent. of the vertical lobe removed before attempting to train it to discriminate between 6 cm. diameter black and white circles and testing the effect of altering the punishment and reward.

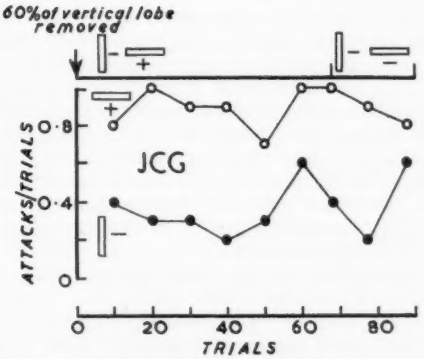

Fig. 8. Similar experiment to Fig. 7 but with 60 per cent. of the vertical lobe removed. (For other details see Boycott & Young, 1957).

end of the day. Attacks on the previously positive figure were still made very frequently and there was, if anything, an increase in attacks on the negative figure. This animal again shows that with reduction in the amount of vertical lobe tissue it is difficult to set up memories that prevent attack on a previously positive figure.

Slow reversal of response also appears in the long experiment with Octopus JAC from which 50 per cent. of the vertical lobe was removed after training to attack a white circle of 6 cm. diameter but not one of 2 cm. (Fig. 9). Performance continued after operation much as before and the animal also learned to attack a vertical but not a horizontal rectangle. After this new pair had been introduced for only

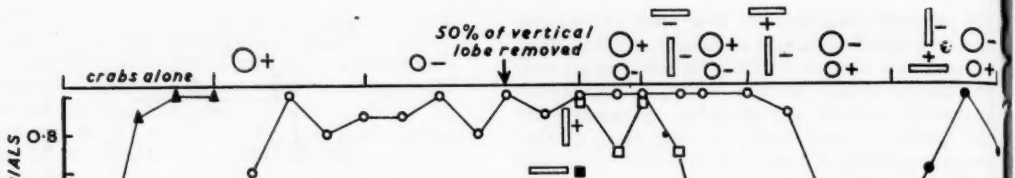

Fig. 9. Octopus trained to discriminate between large (6 cm. diameter) and small (2 cm. diameter) white circles. After 50 per cent. removal of the vertical lobe a discrimination between white 10 × 2 cm. rectangles shown vertically and horizontally was made and various reversal tests carried out. See text. (For other details see Boycott & Young, 1957).

thirty trials shocks were given when the vertical rectangle was attacked and it was rapidly made a negative figure (9 attacks in the next 50 trials). It proved much more difficult to reverse the responses to the large and small cricles, to which the animal had been trained for a long time. Food was given after the showing of the small circle, but in the next thirty trials it was attacked on only two occasions before the crab was shown. Thereafter attacks on it only gradually became more frequent.

Meanwhile shocks were given when the previously positive large circle was attacked and the attacks on it gradually decreased; yet sixteen were made in the next thirty trials, the reversal of response being distinctly slower than with the vertical rectangle, which had served as a positive figure for a much shorter time.

Finally crabs were given after attacks on the horizontal rectangle or after fifteen seconds if there was no attack. Eleven attacks were made in thirty trials, as against only two in thirty for the circle.

This experiment therefore indicates that reversal of response is only slowly learned after reduction of the amount of vertical lobe tissues. Even more important is the demonstration that the difficulty of turning either a "positive" figure into a "negative" or vice versa is greater the longer the previous training in the other direction. This is a further demonstration that the behaviour of the animal depends upon both "positive" and "negative" memories.

Discussion

The earliest experiments in which the effect of the vertical lobe system upon discrimination of shape was studied involved a reversal of response, for the octopuses were trained not to attack crabs when shown with a white square (Young, 1951; Boycott & Young, 1950, 1955a & b). It was not at first appreciated that such learning not to attack crabs is a difficult task for the animal. Memories preventing attacks on crabs can be set up quite quickly but they fade after a few days unless reinforced, and attacks are again made on the crab. Presumably most or all octopusses carry a well-established memory ensuring attacks at crabs. In the present series of experiments the animals were trained for varying periods with figures that were presumed to be at first indifferent (so far as this can be claimed for any figure). Reversal of response was then possible after relatively short re-training and there were no signs of a tendency to revert to the responses originally learned Thus, in an octopus, memories that either promote or prevent attack can be set up when the attributes of a particular figure are presented in association with either food or a shock. The setting up of either of them is made more difficult after removal of part or all of the vertical lobe system, but they can still be established. The learning of a new discrimination is probably abnormally slow after part of the vertical lobe has been removed (Figs. 5-9). Memories set up before operation persist after vertical lobe removal, although the accuracy

of performance is impaired (see Boycott & Young, 1957). Three experiments indicate that reversal of the effects of memories was slow after vertical lobe removal (Figs. 6, 8 and 9). Further experiments are required to resolve the differences between these results and those of Wells & Wells (1957), where reversal to tactile discrimination is faster.

The rates of learning give some insight into the properties of the neuron systems that constitute the information stores. As is to be expected it takes more trials to reverse the responses than to set them up originally. Particularly it is hard to reverse a memory that prevents attack. This effect appears most dramatically in the experiments described on p. 3 in which giving food with the figure that was originally negative has the effect of stopping attacks on the figure from which food was previously received! This apparently paradoxical result can be explained on the hypothesis that the effects of the crab given in both situations in this particular way is to link the memory preventing attack with both figures.

The rate at which the new response is learned following reversal of reward and punishment is approximately inversely proportional to the time for which the original training had lasted. This appears especially clearly in the experiment of Fig. 9, with an animal with a reduced amount of vertical lobe tissue.

Unfortunately we still remain ignorant of the nature of the processes by which representations of the visual attributes of a situation are set up and promote or prevent attack. There is evidence, however, that they depend upon the number of neurons available in the vertical lobe system, serving to maintain the memory by re-presentation to the optic lobes (Boycott & Young, 1957). In the absence of the vertical lobe system such memories are set up with much greater difficulty.

Cautious Behaviour During Learning

For many years studies have been made involving the production of experimental neurosis in animals (Pavlov, 1941) and latterly of conflict behaviour (Miller, 1944) and displacement activities (Tinbergen, 1951). These categories of behaviour are produced experimentally in a variety of ways, such as presenting an animal with discriminations beyond its resolving power, situations in which there is competition between opposing tendencies to react, or situations in which the consummation of an activity is prohibited. It is not the purpose of this paper to decide what all these have in common or to what extent, if at all, they are separate categories of behaviour under stress (Russell, 1953).

In our experiments behaviour comparable to that shown in these categories has appeared. This is the first case of its kind recorded in a mollusc or possibly in any invertebrate.

When octopuses are trained to discriminate between a crab and a crab presented with a white square, there is a period in the early stages of training when the animal is "cautious" during an attack on the crab and square and may approach closely to it without attacking (Boycott & Young, 1955a; Boycott, 1954). That there is a transitory overlapping of the various systems of neurons concerned with promoting and preventing the response is shown by the fact that caution may also be shown for a while towards crabs presented alone. Similar behaviour may appear towards the positive and negative figures used in this paper and in other training experiments (Boycott & Young, 1956). In the later stages of training, when an animal has learned not to attack the negative figure, behaviour which fits into the category of a displacement activity may occur. While the negative situation is in the tank the animal pays attention to it, but at the same time picks up pieces of the shells of the crabs of previous meals, takes these to its mouth and rejects them. Also it may suddenly attack bubbles on the surface of the water or a shadow in the tank. We have not kept a systematic account of such behaviour. It does not appear in every animal under the same conditions. It has been noticed more often in the experiments using a crab and crab and square as the discrimination, that is to say when the "positive" element "crab" is a feature of both situations.

In some situations we have seen "withdrawn behaviour" in which the animal remained mostly in its home. Conversely, in other experiments, an octopus was found between training runs to be walking and swimming about the tank and attempting to climb out much more often than would a normal octopus.

The changes in the learned responses that were imposed upon the animals in the present experiments are likely to bring into conflict memory systems so constructed that they indicate opposing responses to the rest of the nervous system. This produces patterns of behaviour that are biologically inappropriate.

In all the animals trained here, no signs of such behaviour were shown in the first part of the experiment. Then when shocks were given after attacks on *either* of the two figures, instead of only one of them, there were at first cautious attacks on the originally positive figure until the animal had learned not to attack this further (Figs. 1 and 2). If then one of these negative figures was made positive the attacks on this figure were at first cautious and frequently the animals would jump back when a crab was put into the tank. It then might be some 60 seconds before a final attack would be made. This behaviour passed off as the animals began to attack the new positive figure more and more readily.

Behaviour of the above kind was also shown when both figures were rewarded (Figs. 2-4). In Octopus JCB this behaviour passed in the last thirty pairs of trials to behaviour which was the most extreme indication of conflict or neurotic behaviour we have observed. When the cover of the tank was moved at the beginning of a set of trials the animal often attempted to climb out. It actually succeeded in doing this six times between trials 93 and 110, making many other abortive attempts. At other times it was often observed to be swimming or walking around the tank in a manner seldom seen in normal octopuses.

These observations show in O*ctopus* behaviour comparable to that known as "conflict behaviour" in vertebrates. It is significant, however, that this behaviour did not appear in those octopuses that had a considerable proportion of their vertical lobes removed, presumably because in these the memory systems promoting or preventing attacks were inadequate to dictate competing responses to the effector systems. Cautious behaviour may, however, appear in such operated animals during tests at short intervals, which establish transitory memories (Boycott & Young, 1955a).

Summary

1. After an octopus has learned to attack one figure but not another the responses can be reversed, but training in the new direction takes more trials than the original training. The longer the previous training the greater the number of trials needed for reversal.

2. If an octopus trained to attack one figure but not another is given food (crabs) after presentation of the "negative" as well as the "positive" figure, it first begins to attack the previously negative figure as well as the positive, but then comes to attack neither. The common factor of crabs given with both figures has attached the attributes of shock to the previously positive figure. Conflict behaviour appears.

3. After removal of most of the vertical lobe there is some evidence that reversal of responses to a pair of figures takes place more slowly than in a normal octopus.

Acknowledgments

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"STRING-PULLING" IN BIRDS. (2) DIFFERENCES RELATED TO AGE IN GREENFINCHES, CHAFFINCHES AND CANARIES

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Introduction

Birds from a wide variety of species are able to obtain food by pulling up a string on which it is suspended. The pulled-in loops may be held by the feet while the bird reaches with the beak for another pull. This apparently skilled behaviour has received considerable attention from ornithologists, and their work has been reviewed and discussed by Thorpe (1943, 1945 and 1956). Thorpe (1956) discusses this capacity in terms of insight learning, tool using behaviour, and an innate behaviour pattern. Altevogt (1953) concluded from observations made on a brood of captive blue tits (*Parus caeruleus*) that string-pulling is based exclusively on an innate feeding pattern involving use of the foot. In a preliminary experiment carried out on wild captive great tits (*Parus major*), individual variations in string-pulling have been analysed in terms of conditioning; failure to learn was associated with the "extinction" of the bird's response to the bait owing to lack of reinforcement (Vince, 1956).

The experiment described here is a continuation of this investigation in a group of finches. Whereas tits habitually use the feet to hold food and other objects and appear to hold pulled-in loops of string quite automatically, finches use the feet in feeding to a lesser degree and for this reason string-pulling may be more difficult for them.

The birds were tested in groups which varied in age, experience and species; the species were chosen to give some variation in strength of response to the bait used. In this paper the effects of these three factors on string-pulling are considered, while Part III of this series discusses the acquisition of the string-pulling capacity in individual birds.

Experimental Procedure

The apparatus used was that described by Thorpe (1956) and Vince (1956) and is shown in Fig. 1. It consisted of a horizontal perch 12″ long, fixed to a retort stand. A piece of red string 4″ long was attached to the top of the perch by a drawing pin and suspended inside a glass cylinder 1.7″ in diameter on which the perch rested. A clamp holding the glass cylinder made a second perch parallel with and 7″ below the first. A small piece of chickweed (*Stellaria media*) provided the bait and was attached to the free end of the string. The glass cylinder was used to prevent the bird from snatching directly at the chickweed.

The birds were kept singly in flights measuring approximately 3′ x 3′ x 3′, and indoors. They were moved to these flights containing the apparatus some days before the preliminary training began. The birds were not deprived of food before being tested, in fact, food and water were left in the flights all the time and in this respect the conditions differed from those described by Thorpe (1956) and Vince (1956). They were, however, not given chickweed except during the training and test periods.

The experimental period was divided into two: (1) an initial period in which the bird was trained to take chickweed from the experimental perch and (2) the test period with chickweed suspended from the 4″ string.

(1) The Training Period

A small piece of chickweed was attached to the perch by a drawing pin at the point where the string would be fastened later. Some birds (chiefly canaries) went to the perch quite quickly and took and ate the bait, some approached the perch only after considerable delay and some (all adult hand-reared chaffinches) failed to take the bait at all. This training procedure was repeated, usually three times a day, until the latent period (time within which the bait was touched) showed no sign of diminishing further. The birds were thus given different amounts of training with the aim of equating the latency of their response to the bait. All times were measured to the nearest half second. Timing began when the experimenter had returned to a seat after placing the test object in the flight.

(2) The Test Period

The experiment was divided into twelve test trials, each lasting half an hour, and given on days which were as nearly as possible consecutive. In a few cases the number of tests given was less than twelve: these were (1) birds which succeeded in pulling up the string and obtaining the bait, (2) birds which ceased to respond and for two consecutive half hour tests failed to alight on the experimental perch or clamp and (3) a group of hand-reared greenfinches tested for only six days. Testing began when the 4″ red string with a small piece of chickweed attached was pinned to the perch and suspended inside the glass cylinder, and during the subsequent half hour as far as possible all the bird's behaviour was recorded and timed.

(3) Age, Species and Early Experience

In all, forty-nine birds were tested; sixteen chaffinches (*Fringilla coelebs*), eighteen greenfinches (*Chloris chloris*) and fifteen domestic canaries (*Serinus*), Border strain. They were divided into ten groups according to species, age and experience as shown in Table I.

There were three groups of chaffinches:

TABLE I

Greenfinches				Chaffinches			Canaries		
Wild Adult	Juvenile			Wild	Hand-reared			Juvenile	
	Aviary-reared	Hand-reared 1953	Hand-reared 1955	Adult	Adult	Juvenile	Adult	String	Wire
(1). Number which failed preliminary training—not tested.									
0	0	0	0	0	5	0	0	0	0
(2). Number tested in each group.									
6	5	4	3	6	4	6	6	5	4
(3). Age at which tested.									
not known	8-26 wks.	8 weeks	7 weeks	not known	2nd or 3rd year	8-23 wks.	not known	15-17 wks.	18-22 wks.
(4). Mean number of trials required for training to shortest latent period.									
13	17	not known	6	12	13·2	9·2	6·3	5·9	
(5). Mean shortest latent period in training trials.									
4·2 secs.	9·5 secs.	not known	2·6 secs.	2·5 secs.	9·5 secs.	5·3 secs.	0·2 secs.	0·1 secs.	
(6). Time interval before going to perch or clamp in test trial. I.									
11·3 secs.	14 secs.	not known	193 secs.	182·5 secs.	533 secs.	757 secs.	2·2 secs.	not known	0 secs.
(7). Trial in which string or pin was first touched.									
2·5	2·6	1·3	1·3	6	6·5	3·3	2·5	1	
(8). Average time spent on perch or clamp.									
50·7 secs.	213· 6secs.	519 (Six sessions only)	297 secs.	68·5 secs.	139·5 secs.	163·7 secs.	147 secs.	477 secs.	328 secs.
(9). Number which pulled up the string in 12 test trials.									
0	1	(Six 0 sessions only)	2	0	0	0	0	5	not possible
(10). Number which became extinguished in 12 trials.									
3	1	—	0	2	1	0	1	0	0

PLATE II

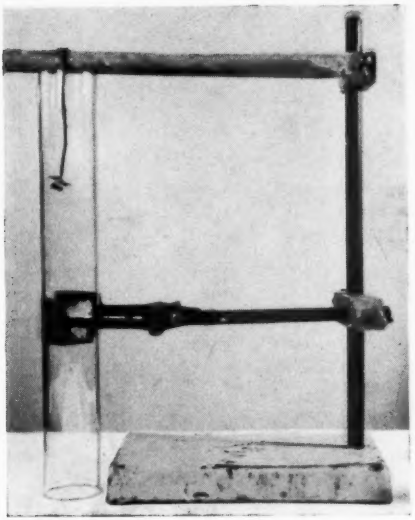

Fig. 1. Experimental apparatus

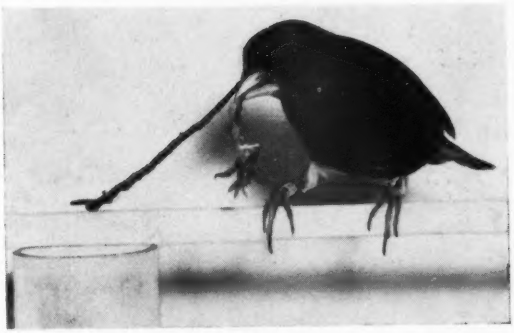

Fig. 2. Successful response by male greenfinch

(1) six wild caught adults, (2) four adults in their second or subsequent year which had been taken from the nest and reared by hand and (3) six hand-reared juveniles tested at ages ranging from eight to twenty-three weeks. In addition there were five adult hand-reared chaffinches which failed to take chickweed from the perch during the training period and so could not be tested. These appear in a separate category in Table I and are not included in the forty-nine.

The greenfinches fell into four groups: (1) six wild caught adults, (2) five juveniles reared by their parents in an outdoor aviary and tested at ages ranging from eight to twenty-six weeks, (3) four hand-reared juveniles tested at eight weeks (the 1953 group) and (4) three hand-reared juveniles tested at seven weeks (the 1955 group).

Of the canaries, group (1) comprised six adults, (2) contained five juveniles tested between fifteen and seventeen weeks and (3) four juveniles tested between eighteen and twenty-two weeks. The juvenile canaries in group (3) were tested with chickweed on the end of a 4″ red wire instead of string. The wire could not be pulled up and therefore their response to the bait was never reinforced by feeding.

The hand-reared juvenile greenfinches and the juvenile canaries had all been kept without access to grasses, cotton and any other objects from which they might have obtained experience relevant in the string-pulling situation. Only the wild adult birds and aviary-reared greenfinches had the more varied experience of being reared and living out of doors; these birds were easily disturbed and were watched from behind a screen during the training and test periods, but this proved not to be necessary with the canaries and hand-reared birds.

Results

Figure 2 shows a male greenfinch pulling up the string by nibbling along it. Some birds used this method and others held a loop with the foot while pulling in the string.

The results are summarised in Table I, most of the data being presented in average figures for each group. These will be considered under four headings. The first deals with the measure of success achieved in string-pulling by birds of different species, age and experience, and the following three with other factors which could contribute to success, so that (2) considers variations in the initial training period, (3) the length of time spent responding during the test trials and (4) the effect of rearing birds with no access to string-like material.

(1) Measure of Success Achieved

Table I indicates the number of birds in each group which succeeded in obtaining the bait during the twelve test trials. The results are striking: no adult bird succeeded; no chaffinch of any age was successful; among the juveniles all five canaries tested with string and (omitting the four given only six trials) nearly half the greenfinches became proficient at string-pulling.

(2) Differences in the Training Period

Table I gives average figures indicating variation in the rate at which different groups learned to take chickweed from the experimental perch, and also the intensity of their response to the bait as indicated by the length of their latent period. These data show that the canaries learned more rapidly and had a shorter latent period than the other birds. The figures given for hand-reared adult chaffinches are biassed in their favour by the fact that five of the nine birds originally in this group failed in the preliminary training and their results are omitted from the averages. Although they would eat chickweed from the floor of their flights, none of the five ever alighted on the experimental perch and took it from there. Their approach to the bait was weak initially (chaffinches are rarely seen to eat chickweed in the wild), but increased after eating it several times on the floor. These chaffinches responded at first to chickweed placed on the experimental perch by flying near, or looking and stretching towards it. Later this unreinforced response to the chickweed ceased and tests were abandoned.

(3) Duration of Response in the Test Trials

There are many ways in which the bird's response in this situation may be scored. For the present only the length of time spent during each half-hour trial on the experimental perch or on the clamp below it will be considered, and presence on perch or clamp will subsequently be referred to as the birds' "response." Time spent on the clamp is important as in this position the bird was very close to the bait. In Fig. 3 the average time spent on the perch or clamp in each test trial has been plotted for each group of birds and average figures for all test trials are given for the various groups in Table I.

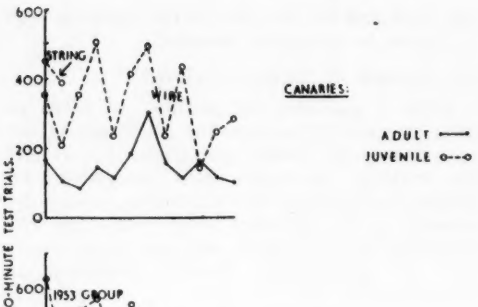

Fig. 3. Changes in responsiveness during 12-day test period

These figures reveal a marked difference between the behaviour of the adult, and juvenile birds. The young birds spent a much greater proportion of the test period in responding than did the adults. In some cases this difference was apparent in the first test trial, and in others the response of juveniles and adults was approximately equal in the first trial, but that of the juveniles later increased. It could be inferred from this that the response of the juveniles in the experimental situation was more intense than that of the adults. This greater responsiveness of the juveniles may well have contributed towards their greater success in string pulling.

Other differences in Table I could support the view that the younger birds were more responsive in general than the adults. During test trial 1 when chickweed was presented for the first time on the string, the young birds were on the whole slower than the adults in approaching perch or clamp, a difference which could be due to a more intense avoidance response to strange objects in the younger birds. Once on the perch the response of the juveniles again appeared to be the more intense as they pulled at or touched the string or drawing pin holding it sooner than did the older birds.

There is another effect which could contribute towards the greater success of the young birds. It may be seen from Fig. 3 that the curve showing time spent responding by the adult greenfinches tends towards zero. In fact, three of the six birds in this group ceased to respond before the end of the test period. Two of the wild adult chaffinches and one of the adult canaries also ceased to respond, although in their case the tendency towards zero does not show up in the averages. Only one juvenile (an aviary-reared greenfinch and the oldest of the young birds) stopped responding before the end of the test trials.

This failure of the unreinforced response to become extinguished in the young bird is, however, apparent only when the whole test period is considered as in Fig. 3. When the daily scores are analysed it is found that the birds' response fell off markedly during each half-hour trial, and this effect occurs in juveniles as well as adults. Figure 4 shows the time spent responding over five-minute periods in each half-hour test trial in the adult and juvenile groups of canaries. Here the curves are mostly L-shaped, showing that the birds responded most continuously at the beginning of each half-hour. Sometimes the response revived to some extent

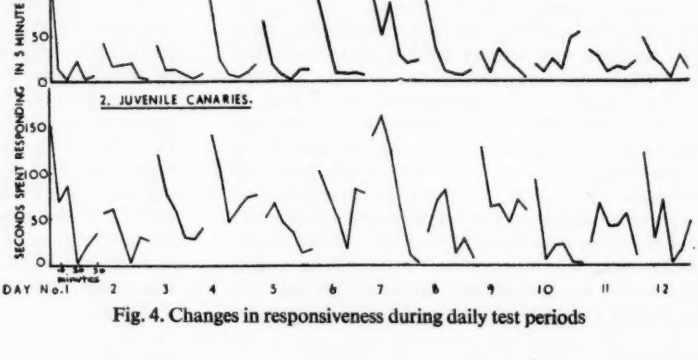

Fig. 4. Changes in responsiveness during daily test periods

towards the end of the half-hour period. It seems that extinction of the unreinforced response occurred in all the birds, but was less stable in the juveniles, as the response revived in their case during the twenty-four-hour interval between test trials.

There are two groups of birds tested whose results are somewhat anomalous. The irregularity of the curve in Fig. 3 representing aviary-reared greenfinches is due to their responsiveness increasing over the first few trials to a level above that of the other juveniles, and then tending towards zero, the individual peaks being reached on different days. These birds differed from the other groups in that the average duration of their response was similar to that of the other juveniles but the tendency towards extinction was similar to that of the adults. The adult hand-reared chaffinches showed a similar type of variation.

The group averages given in Table I show that the greater success of the juveniles in string-pulling is associated with the greater length of time spent by them in responding to the bait and/or string. Individual results show that, omitting the four greenfinches given only six trials and the four canaries tested with wire instead of string, and considering only the trial in which each bird gave its maximum response, none which spent less than 400 seconds in responding was successful (21 birds). But duration of response is not the only factor contributing to success. The eight birds which were successful had a maximum between 400 and 1300 seconds, but twelve unsuccessful birds also gave maximum scores between 400 and 1780 seconds.

(4) Effect of Rearing Without String-like Material

The hand-reared greenfinches and juvenile canaries had been reared without access to grasses and string-like material from which they might have obtained experience useful in the string-pulling situation. This early lack of experience seems, however, to be irrelevant to the experiment as these birds were the most successful in string-pulling.

Discussion

The results have shown that juvenile birds were superior to adults in the string-pulling situation, and that success was correlated with the amount of time spent responding to the string and/or bait.

In an earlier paper (Vince, 1956), string-pulling in wild adult great tits was considered in terms of conditioning; it was suggested that success depended on the intensity of the bird's response to the bait which increased and then decreased if the bird failed to pull up the string and the response to it was unreinforced. The disappearance of the response was considered to be an example of extinction, and the initial increase to be due to the dying away of the bird's fleeing response to a strange object and/or to the effect of the sight of food as secondary reinforcement. Similar effects occurred in the present experiment. In the present experiment, however, where the birds tested were a less homogenous group than before, two new features emerge in the results: the young birds were more responsive than the adults and extinction was less stable in young than in older birds.

The responsiveness of the young birds may be compared with activity and learning capacity in the rat. It has been shown that young rats are more active than older rats, and in fact there is an optimum age for activity at about three or four months (Slonaker, 1912; Richter, 1922). An optimum age for learning, mostly in the maze, has been demonstrated by Watson (1903), Hubbert (1915) and Liu (1928), the peak occurring at about 75 days. This work, however, is not entirely consistent as in different types of learning situation Watson (1903) and Maier (1932) have found older rats superior to younger. In addition, Stone (1929 a & b), who has carried out the most detailed experiments in this field, has demonstrated that by feeding them with a very severely restricted diet he was able to raise the level of performance of older rats to that of the younger ones. Under conditions of more moderate hunger "drive" the younger rats were superior. Stone concluded from these experiments that the age differences found in learning experiments are explicable in terms of a motivational change.

In the present experiment the birds were allowed to feed normally and hunger "drive" will have been low throughout; according to Stone's results, therefore, the effect relating to age was to be expected. In fact the differences observed could be attributed to different levels of motivation in older and younger birds if the increased latency of response in the younger birds in test trial I, is, as suggested earlier, due to the dying away of an initial avoidance response to a strange object (the string), which, if *all* responses are more intense in younger animals, will also be more intense in their case than in that

of the adults. But a more detailed analysis of the results as a whole suggests that the motivation type of explanation conceals a number of problems which need further investigation.

There are two main questions which arise from this experiment. The first relates to the waning of the bird's response in the unreinforced situation. This was seen to occur in all birds in separate half-hour trials, but to be maintained from day to day almost exlusively in the adults. If this effect is, in fact, an example of Pavlov's extinction of conditioned reflexes, then it appears to be unstable, or short-lived in the juveniles, and more stable in adults. The question arises as to whether this effect is peculiar to birds and to extinction, or whether it is characteristic of internal inhibition and occurs in other animals. There is evidence which suggests that the age effect observed is of general significance. Pavlov (1927) has demonstrated a practice effect in the establishment of extinction in dogs and this has been confirmed by Ellson (1940); also "learning set" experiments (Harlow, 1950) have revealed a similar effect in discrimination tasks in monkeys. Further, Frolov's assertion (Frolov, 1937) that internal inhibition is weak in young animals and strengthens with age, has been confirmed in the establishment of differentiations by Panchenkova (1956) in rats and in children by Paramonova (1955). Similar effects supporting this view, but obtained from various different experimental tasks have been reported by Luria (1932), Lambercier & Rey (1935) and Rey (1954), all working with children.

The second question raised is that of factors underlying the difference observed. Is the process observed one of maturation? So far as they go the data suggest that experience at least contributes to differences related to age. For example, the young aviary-reared greenfinches had a greater tendency towards extinction than young hand-reared or more restricted birds, and in this respect they were more like the adults. Owing to the large number which failed the initial training the results of the chaffinches are difficult to interpret. The adult hand-reared birds had some tendency towards extinction, like the wild adults, but in average duration of response the adult hand-reared chaffinches came between wild adults and hand-reared juveniles. On the whole the tendency towards extinction showed an increase with age, or with increase in experience or variety of early environment. Much more evidence is needed on this point, but it is consistent with the observations of Pavlov, Ellson and Harlow mentioned above, and also with the results of Thompson & Heron (1954 a & b) who have varied the experience of dogs by rearing them under different degrees of restriction. Thompson & Heron found that dogs reared under restricted conditions later behaved more like young dogs than normal adults.

Summary

Groups of finches were tested in the "string-pulling" situation. Success in this situation varied according to the species, age and experience of the birds tested, and was related to the length of time spent responding to the string and/or bait.

The results raise a number of questions which are discussed in a preliminary manner. They suggest (i) that internal inhibition in Pavlov's sense is unstable in young birds and (ii) that the process of development from the unstable type of inhibition found in younger birds to the more stable type found in older birds may depend on experience as well as age.

Acknowledgments

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A FIELD STUDY OF THE POTASSIUM CONCENTRATION IN THE BLOOD OF THE RED LOCUST *Nomadacris septemfasciata* (Serv.), IN RELATION TO ITS ACTIVITY

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It is known that in *Locusta* a high concentration of potassium reduces the end-plate potential and the muscle spike-action potential so that smaller muscle contractions result on excitation via the nerves (Hoyle, 1954). Hoyle has shown that the potassium concentration in locust blood is increased after feeding and has related this to the reduced state of activity after feeding (see also Ellis & Hoyle, 1954).

Chapman (1957) commented on the build-up of high-density populations of adult Red Locusts, *Nomadacris septemfasciata* (Serv.), in the grass plains of the Rukwa Valley, Tanganyika, by a process of "real" concentration (Kennedy, 1939) and suggested that this was related to the vegetation, which was important for its food value as well as its physical properties. The locusts congregated in areas dominated by *Echinochloa pyramidalis*, a tall grass for which they showed a distinct preference in laboratory experiments on feeding. The reasons for this congregation are not known. The variety of external stimuli to which the locusts were subjected undoubtedly differed markedly in different habitats, and the relative lack of activity in any one type of habitat might be attributed to such differences, but the work of Hoyle suggested that this congregation, which was the result of an active movement by the locusts, might be related to the potassium content of the locust blood, and this, in turn, to the potassium status of the food grasses.

An investigation of this possibility was undertaken in the Rukwa Valley, Tanganyika Territory, which is a permanent outbreak area of the Red Locust. Unfortunately 1956, when the work was carried out, was a poor locust year and no large-scale displacements or congregations were observed. The programme was, therefore, limited to an investigation of the daily and seasonal variation in the concentration of potassium in the locust's blood and an attempt was made to relate this to the state of feeding and the daily flights from and to the roosts.

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Methods

The observations and collections of locusts were made in low-density adult populations from June to December, 1956. In June and July the locusts were in an area dominated by the grass *Hyparrhenia rufa;* from August onwards they were in an area dominated by *Sporobolus robustus* which remained unburnt throughout the observations, although the rest of the plains was burnt. Very little *Echinochloa* was present in either area. The observations on flight activity consisted of counts of the numbers of locusts crossing a given line in a three-minute period, counts being made at 15-minute intervals throughout the day (see Chapman, in press). Activity could not be estimated on the same day as the blood was analysed but the variation in day-to-day behaviour was so slight that the results may justifiably be compared.

For the determination of blood potassium an Eel flame-photometer was used. A batch of about 50 locusts for analysis was collected every three hours during the daylight hours, starting at 06.00 hours. They were immediately brought back to the laboratory, a journey of about 30 minutes, and the blood was extracted and analysed. A cut was made in the thin cuticle immediately behind the pronotum, and the locusts were then left for five minutes. At the end of this time a drop of blood had usually accumulated at the cut and 2 cu. mm. was withdrawn into a haemocytometer pipette suitably graduated. Loss of moisture by evaporation from the blood during this period was of no significance. Had it been important, the potassium concentration in the last of each set of samples would have been greater than in the first since it had more time in which to evaporate. In fact, the values were very similar, the mean of the first sample being slightly higher (first $n=62$, $\bar{x}=18.11$; last $n=62$, $\bar{x}=16.9$). The dilution necessary for use with the flame photometer was too great for the insects to be tested individually and for reliable results it

was found most satisfactory to dilute 2-cu.mm. samples from ten locusts in 3 ml. of distilled water. A series of samples was taken twice each month.

Checks of the accuracy of volume measurements were made by weighing. The maximum error obtained in measuring ten samples of 3 ml. of distilled water was 2.3 per cent. with a standard deviation of 1.4 per cent. The maximum error in measuring ten batches each of ten samples of 2 cu.mm. was 7.0 per cent. with a standard deviation of 3.7 per cent. The reproducibility of the flame-photometer results was determined by repeatedly testing standard solutions. At the upper end of the range used the maximum deviation from the mean value obtained was 4.0 per cent. with a standard deviation of 2.3 per cent. (n=10) and at the lower end the maximum deviation from the mean was 2.3 per cent. with a standard deviation of 1.8 per cent. (n=10). No account was taken of interference by other ions.

The state of feeding was determined from the oesophageal contents of the locusts whose blood was used for analysis. The oesophagus was classified as being "full", containing "some" food or "empty", these states being scored 2, 1 and 0, respectively. The sum of the scores for the whole sample was then expressed as a percentage of the possible maximum if all the locusts had been fully fed, scoring 2 each (see Chapman, 1957).

Blood Potassium Concentration of Field Samples

There was a regular daily increase and decrease in the concentration of blood potassium of the locusts (Fig. 1). The level of potassium rose from about 15 m.equiv.K/litre of blood in the early morning sample to about 20 m. equiv.-K/litre during the heat of the day, falling off again in the late afternoon. Only on one day was there no marked increase in a series of 13 observations. The changes were observed in both males and females. Taking the early morning values as the basic level, mean values of 15 m.equiv.K/litre of blood are obtained for both sexes (n=37, n=20). This is in good agreement with Hoyle's (1954) mean figure of 11 m.equiv.K/litre of blood for starved adult *Locusta* in the laboratory.

The increase in the concentration of potassium was not obviously related to the state of feeding. Feeding was often in progress in the mornings at the time of the initial increase in potassium concentration but was reduced over mid-day, when the concentration was at its maximum. The main meal was usually taken in the late afternoon when the level of potassium was falling again.

Nor was there any obvious relation between potassium concentration and flight activity, except that the mid-day reduction in flying corresponded with the highest concentrations of potassium. The outward flights from the roosts were observed at a time when the concentration of potassium was increasing and the return flights when it was decreasing.

During the heat of the day many of the locusts did not contain sufficient blood to be used in the samples. Hence in Fig. 1, relatively few estimates of potassium are available for the mid-day period. In males there was a positive correlation between the concentration of potassium and the percentage of locusts with insufficient blood (r=0.51, t=6.30, d.f. 113, 0.001>P). A similar effect was apparent in females but, being larger than the males, they

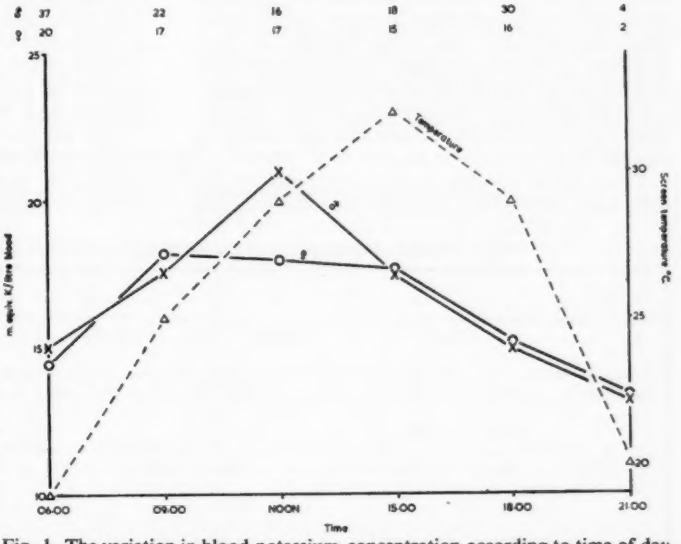

Fig. 1. The variation in blood potassium concentration according to time of day. (Mean values for the months of June to December with the mean screen temperature for the same times; the figures at the top indicate the numbers of estimations on which each point is based.)

had a greater blood volume and it was usually possible to obtain 2 cu.mm. Hence the correlation between potassium concentration and the percentage of females with insufficient blood was not significant. The percentage of males with insufficient blood was in turn correlated with the screen temperature at the time. of collecting ($r=0.55$, $t=5.02$, d.f. 58, $0.001>P$)

This suggests that the changes observed in potassium concentration were related to loss of water by the locusts and that changes due to feeding were not great. However, on two occasions the sodium concentration in the blood was also determined. This could not be done regularly, as was desirable, because the dilution required for testing sodium was greater than that for potassium. For the determination of sodium, 2-cu.mm. samples from each of ten locusts were diluted in 6 ml. of distilled water. Further difficulty was experienced in avoiding contamination in the dust-laden atmosphere. It was found that the concentration of sodium did not show changes comparable with those in potassium level, but remained relatively constant (Table I). This suggests either that the changes in potassium were not related to moisture content, since in this case the sodium would have varied similarly, or that regulation of potassium was much slower than that of sodium. The work of van Asperen & van Esch (1956) showed that rapid regulation of sodium occurred in the reverse manner when water was injected into the haemolymph of *Periplaneta* and there was some evidence that sodium was decreased when large quantities of potassium salt were injected. It is, therefore, possible that rapid regulation of sodium did occur in the locusts.

However, it became apparent that changes in potassium concentration might be related to the degree of handling of the locusts on capture. In the cool of the mornings and evenings collecting was relatively easy but in the heat of the day it became very arduous. At this time the locusts caught tended to be roughly treated before being caged, while the collectors pursued other locusts. The African scouts, who collected the locusts, could see no reason to be gentle with them. On three occasions comparisons were made of the potassium concentration of locusts collected by the Africans in the usual manner and that of others which were handled very carefully and caged immediately on capture. In females the level of potassium was similar in both cases but in males the concentration was distinctly lower in the carefully treated locusts (means 19.4 and 15.5 m.equiv.K/litre of blood, $t=4.36$, d.f. 10, $0.01>P>0.001$). This was realised too late to modify the methods of collecting the routine samples.

Consequently it is not known if the daily increase in the level of blood potassium was a natural occurrence or if it was produced artificially by rough handling of the locusts. Marked fluctuations, however, did occur and a few experiments were carried out in the laboratory to determine the factors affecting the concentration of potassium.

Cage Experiments

The experiments to be described were carried out in a field laboratory. It was impossible to control accurately the conditions to which the locusts were subjected; the results therefore cannot be regarded as conclusive but merely as suggesting a need for further work.

For all the experiments, locusts were freshly collected every morning at a time when the effects of handling were not apparent. On being brought into the laboratory they were

Table I. Sodium Concentration of Locust Blood, expressed as m.equiv.Na/litre of Blood

Date	Time									
	06.00		09.00		12.00		15.00		18.00	
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
16/XI	108	116	92	114	?	90	?	?	?	?
	114	102								
15/XII	70	72	?	78	86	72	66	72	64	70
	56			66		66				
	54									

Table II. Potassium Concentration in Blood of Locusts Starved in the Laboratory

Date	Time											
	09.00 K			12.00 K			15.00 K			18.00 K		
	♂	♀	Temp. °C	♂	♀	Temp. °C	♂	♀	Temp. °C	♂	♀	Temp. °C
13/VIII	13·5	13·5	25	13·5	15·4	27·5	13·5	9·6	30·5	16·3	15·4	28
	13·5	12·0		12·5	9·6		10·5	11·5		11·5	12·5	
	14·4			12·5			13·5			10·6		
14/VIII	12·5	12·5	25·5	11·1	11·5	28·5	12·5	14·4	29·5	10·6	14·4	28·5
	12·5	12·5		11·5	11·5		13·4	10·9		12·5	14·4	
	10·9			11·1			9·7			10·0		
15/VIII	15·4	14·4	26	11·5	12·5	29	14·4	13·4	30·5	14·0	12·5	28·5
	13·4	12·5		14·0	12·5		12·5	12·5		13·4	11·3	
	11·3			14·4			14·9			11·8		

In this and all subsequent tables the concentration is expressed as m.equiv.K/litre blood.

sorted into 12-litre cylindrical cages, 50 locusts per cage.

In the first series of experiments, the locusts were kept in the laboratory all day without food and samples for analysis were removed at three-hourly intervals. Temperatures did not fluctuate as much as in the field and at no time was difficulty experienced in obtaining sufficient blood. The locusts were not given water to drink in this or any of the other experiments, except when the effects of drinking were being specifically studied. Under these conditions the concentration of potassium remained constant throughout the day (Table II). This showed that the changes observed in the field samples were not long delayed effects from previous feeding and suggested that they were due either to the rough handling or to greater temperature changes.

Extending the period of starvation over one or two days did not cause a drop in the potassium concentration. There was, in fact, a suggestion of an increase (Table III). The percentage of locusts with insufficient blood for the samples

Table III. Potassium Concentration in Blood of Locusts after Prolonged Starvation, and also the Percentage with Insufficient Blood (%)

Date	1st Day				Starved 1 Day				Starved 2 Days			
	♂		♀		♂		♀		♂		♀	
	K	%	K	%	K	%	K	%	K	%	K	%
17/IX	19·2	5	14·4	0	19·2	63	21·6	50	21·3	78	?	?
	15·4		14·8									
24/X	16·3	9	12·5	0	19·2	29	20·2	33	?	?	?	?
	12·5		15·4		17·3							
31/X	22·1	12	16·3	0	24·0	53	18·3	20	?	100	25·6	10
	15·4		17·3				19·3					
	19·2											

Table IV. Potassium Concentration in Blood of Locusts Exposed to High Temperatures in Cages without Food. (Percentages with insufficient blood expressed under %.)

WITHOUT WATER

Date	Start ♂ K	%	Start ♀ K	%	Temp °C	Exposed 2 hours ♂ K	%	Exposed 2 hours ♀ K	%	Temp °C	Exposed 3 hours ♂ K	%	Exposed 3 hours ♀ K	%	Temp °C	Exposed 4 hours ♂ K	%	Exposed 4 hours ♀ K	%	Temp °C
21/VIII	13·4	4	9·6	0	?	13·4	38	12·5	14	43	?	?	?	?	?	?	?	?	?	?
	11·1		11·8			10·9		12·6												
	11·5																			
28/VIII	16·3	0	12·5	0	25	10·6	23	11·1	0	45	?	?	?	?	?	13·9	43	17·0	50	47·5
	14·0					11·6														
	11·1					12·2														
29/VIII	12·5	6	13·4	0	26	16·3	18	18·2	0	45	18·3	35	16·8	10	43	?	?	?	?	?
	13·4		13·6			23·0		15·1			20·6		19·2							
	15·4					11·1							13·3							

WITH WATER

Date	Start ♂ K	%	Start ♀ K	%	Temp °C	Exposed 2 hours ♂ K	%	Exposed 2 hours ♀ K	%	Temp °C	Exposed 5 hours ♂ K	%	Exposed 5 hours ♀ K	%	Temp °C
31/VIII	14·4	9	12·5	0	24	11·0	12	11·6	0	36	9·6	2	10·6	0	37
	13·4					11·6					10·6				
	14·0					11·6					10·5				
1/IX	14·4	9	10·6	0	24·5	9·7	5	10·6	9	37	9·6	3	11·6	0	40
	13·0					11·6					12·5				
	14·4					12·5					11·6				
						11·6					9·6				
4/IX	14·4	4	13·4	0	24	10·6	0	10·6	0	35	11·5	3	9·6	0	40
	11·1					12·0					10·6		6·7		
	12·5					12·5					8·5				

rose sharply after a day of starvation, suggesting that the increases in potassium concentration were associated with loss of moisture and a decrease in blood volume.

In another series of experiments the caged locusts were placed in the sun without food. During the period in the sun they were subject to very high temperatures, which were measured with an unscreened mercury-in-glass thermometer. There was an indication of an increase in the concentration of potassium in some cases (Table IV), but this was not as marked or as constant as that in the field samples, although locusts were subject to much higher temper-

Table V. Potassium Concentration in Blood of Locusts given Food for Two Hours. (Percentage of food in oesophagus expressed under %.

Date	Start					Fed					Fed + 3 hours					Fed + 5 hours				
	♂		♀			♂		♀			♂		♀			♂		♀		
	K	%	K	%	Temp °C	K	%	K	%	Temp °C	K	%	K	%	Temp °C	K	%	K	%	Temp °C
5/IX	13·4	3	13·4	5	27	13·4	75	12·5	90	27	13·4	27	13·4	35	30	13·4	10	12·5	18	31
	11·5					13·4					12·0		11·1			14·4				
	13·4					12·5					14·4					11·1				
						11·6														
6/IX	11·5	5	13·4	3	27·5	12·5	55	9·6	80	28·5	11·5	30	14·0	35	31	11·5	30	12·5	10	32
	11·5		13·0			9·6					12·5					8·3				
	12·5					11·5					13·4									
						9·7														
7/IX	10·6	5	8·7	0	26·5	11·5	75	11·5	67	28	7·5	17	11·5	5	31	10·1	3	10·6	25	32
	9·6		9·7			9·6		9·8			10·6					8·7		9·7		
	8·7					6·8					10·6					9·6				
											9·6									

atures than in the field. The percentage of locusts with insufficient blood increased as the period of exposure became longer and many of them died.

This experiment was repeated, but the locusts were given ample water to drink, soaked cotton-wool being maintained in the cages. This had the effect of reducing the temperatures slightly but they were still very high. The locusts examined had the gut distended with water and produced blood copiously, the percentage with insufficient blood being negligible even after five hours in the sun. In nearly all cases the potassium concentration in the blood was reduced slightly (Table IV).

Considering the results of these experiments together, there is a good deal of evidence to suggest that the potassium concentration in locust blood is related to water loss and blood volume. Under conditions likely to produce water loss, such as exposure to high temperatures, the potassium concentration tends to rise; with conditions favouring water absorption it falls. These changes, however, are not great and regulation must be very efficient. Injection of water is known to reduce the concentration of calcium and magnesium in the blood of *Periplaneta* for periods of more than an hour (van Asperen & van Esch, 1956).

Feeding was shown not to result in an increase in the potassium concentration. Caged locusts presented with *Echinochloa* leaves for two hours fed avidly, as was shown by the percentage of food in the oesophagus. There was no resulting increase in blood potassium, either immediately after feeding or after an interval of five hours (Table V). The post-prandial resting period lasts for about one hour after feeding at 30°C. so that, if this was necessarily associated with the potassium concentration in the blood, a rise in potassium level would be expected immediately after feeding.

A rough estimate of the amount of grass eaten was obtained by weighing gut contents immediately after feeding. Only fresh grass from the oesophagus, crop and mid-gut was taken, the grass from ten locusts being weighed together and the mean value taken. The mean weight eaten per locust by 30 males was 130 mg. and by 20 females 160 mg. For convenience a figure of 150 mg. is used in the following calculations.

The dry weight of the grass used in the experiment was 33 per cent. of the wet weight (mean of five observations) so that each locust consumed about 50 mg. dry weight. The potassium content of *Echinochloa* was 1.65 per cent. of the dry weight (mean of two observations) so

that the intake of potassium by each locust was about 0.82 mg.

Hoyle (1954) gives a maximum estimate of blood volume in *Locusta* as 0.2 ml. The blood volume of *Nomadacris* can rarely have been as great as this, although the animal is larger, but it is convenient to use this figure. The mean basic potassium concentration in the blood was 15 m.equiv.K/litre (p. 61) giving a value for the total blood potassium of 0.12 mg. It is not known what percentage of food eaten was absorbed, but at a maximum, nearly seven times the basic value would be added to the blood at a meal.

The grass having a moisture content of 67 per cent., about 0.10 ml. of water would be added to the blood volume at the same time, if all the moisture was absorbed. The blood volume would be increased to about 10 per cent. while the potassium content increased to 800 per cent. Hence a marked increase in the potassium concentration would be expected even if only a relatively small fraction of the nutrients were absorbed into the blood. That no such increase was observed indicates an efficient regulating mechanism.

Attempts to evaluate the efficiency of the regulating mechanism by presenting the locusts with cotton-wool soaked in solutions of various concentrations of KCl were not successful. Given a 3M KCl solution to drink, all the locusts were dead or very adversely affected within 45 minutes. A less marked reaction resulted with a 1M KCl solution but many locusts were paralysed, the concentration of blood potassium rising to over 50 m.equiv./litre blood. With a 0.5M solution, the detrimental effect was even less marked while with 0.1M solution no ill effects were observed. In this case the results were rather variable but the concentration of potassium was still very high, about 30 m.equiv./litre blood, seven hours after treatment. During this period the locusts were in dry cages; had they been given water to drink, regulation might have been more rapid.

In a final series of experiments, locusts were fed on a variety of different grasses and a common sedge for a week before their blood was analysed. The five grasses most abundant on the locust plains were used; they were *Echinochloa pyramidalis*, *Sporobolus robustus*, *Hyparrhenia rufa*, *Cynodon dactylon* and *Diplachne fusca*, and the sedge was *Cyperus longus*. Ten locusts were placed in each cage, and five cages were set up for each grass, three containing male locusts and two females. Locusts that died were replaced each day from a sixth cage of each grass, in which larger numbers of locusts were maintained as a stock. The locusts were not given water to drink.

The results are given in Table VI. In both sexes the lowest concentration of potassium was obtained from the locusts fed on *Echinochloa*. The highest value, 29.0 m.equiv.K/litre blood, was from *Diplachne*-fed locusts, being approximately twice that of those fed on *Echinochloa*, but mortality was so high in the *Diplachne* cages that sufficient blood was obtained from only two locusts. The error in determining potassium may, therefore, be considerable in this case. Even neglecting the result from *Diplachne*, a probably significant negative correlation was found between the potassium concentration of the locusts' blood and the moisture content of the grass on which they

Table VI. Concentration of Potassium in the Blood after the Locusts had Fed on Different Grasses, with the Moisture Contents and Potassium Contents of the Grasses.

		Echinochloa	*Sporobolus*	*Cyperus*	*Cynodon*	*Hyparrhenia*	*Diplachne*
Locust blood K	♂	16·3 15·4	16·8	18·3 18·3	21·2 19·2	21·2 19·3	29·0
	♀	14·4	16·3	19·3	16·3	17·3	?
Grass moisture (mean of 4 values) %		65	49	50	41	52	38
Grass K content:							
No. of determinations		2	3	2	2	2	3
% dry wt.		1·65	1·06	1·70	1·25	1·20	1·03

were fed ($r = -0.57$, $t = 2.40$, d.f. 12, $0.05 > P > 0.02$). The potassium content was of the same order of magnitude in all the grasses, between 1 and 2 per cent. of the dry weight, but was greater in *Echinochloa* (1.65 per cent.) than in *Diplachne* (1.03 per cent.). Thus, had the grass potassium been of great importance in determining blood potassium, the results should have been reversed.

Discussion

From these results it appears that the blood volume of locusts is of considerable importance in determining the concentration of blood potassium. In other words, the concentration does not remain constant by regulation as the blood volume changes but rather it seems the absolute quantity of potassium in the blood remains the same so that the concentration varies inversely as the blood volume. However, these are only field experiments and therefore require confirmation and elaboration by more refined techniques. They do, nevertheless, indicate the need for such data and further suggest that a comprehensive study of water relation in locusts would be of value.

The initial problem of whether or not the potassium content of the grasses influenced the displacements of the locusts is partially answered. Had this been the case, the blood-potassium concentration of locusts fed on *Sporobolus* or *Diplachne* should have been markedly less than that of those fed on *Echinochloa*, for the locusts emigrate from areas dominated by the former grasses and concentrate in areas of *Echinochloa* (see Chapman, 1957). This was not the case, the *Diplachne* sample, although unreliable, having a much higher potassium content than *Echinochloa*. This suggests that the potassium in the grass was not the important factor in displacement relative to the vegetation. Clearly a great deal more work is needed before this can be concluded with certainty but it is worthy of note that the potassium content of *Echinochloa* is higher than that of *Diplachne* and *Sporobolus*, as must be the case if the hypothesis is to hold.

Summary

1. A field investigation was made of the potassium concentration in blood of the Red Locust, *Nomadacris septemfasciata* (Serville).

2. The concentration showed a regular increase during the heat of the day. It did not vary with the state of feeding but apparently depended on the blood volume. This was related to temperature but whether directly or because of the effects of rough handling during catching at high temperatures was not determined.

3. The concentration of sodium remained fairly constant throughout the day.

4. Cage experiments confirmed that the blood volume was important in determining the concentration of potassium.

5. No increase in blood potassium was observed after feeding, and this suggests an efficient regulating mechanism. High concentrations of KCl fed to locusts were found to cause paralysis. Recovery after feeding on more dilute solutions was not complete even after seven hours.

6. The experiments provided no support for the hypothesis that the displacement of locusts relative to vegetation areas was related to the potassium content of the grasses concerned.

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THE EFFECT OF EXPERIENCE ON THE MATING BEHAVIOUR OF THE DOMESTIC COCK

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Beach (1948) suggested that in lower mammals and infra-mammalian classes, experience in reproductive behaviour was unimportant for successful fulfilment of that drive. Later, Kagan & Beach (1953) concluded that although practice and learning are unnecessary for biologically adequate coital responses in the rat, their data showed that the sexual behaviour of adult males may be altered by the conditions under which the animals are reared. Valenstein & Young (1955) also found experience to be important in determining the level of sexual behaviour of male Guinea pigs and the efficacy of hormonal therapy.

In birds there is also evidence that experience is effective in shaping the reproductive behaviour of the male. Craig (1914) reported that male Ring-Doves reared in isolation, when first introduced to females, directed their display to the experimenter, thus suggesting that transference of the mating responses had taken place. Räber (1948) also described a case of transference of the mating display of a turkey cock which, although it copulated with turkey hens, showed courtship display to human males only. Also Thorpe (1956) in reviewing the work on imprinting cites evidence that birds imprinted to humans have a tendency when mature to show sexual behaviour towards humans. In chickens Guhl, Collias & Allee (1945) found that two cocks which had been prevented from treading hens by socially dominant males eventually ceased trying to mate even when alone with hens. These results suggest that the sex drive of the domestic cock may be influenced by experimental factors which may account to some degree for the difference in mating and courting frequencies reported by Guhl (1951), Wood-Gush (1954) and Wood-Gush & Osborne (1956). In order to investigate this possibility a number of males were reared under isolation and at sexual maturity their behaviour was compared with a group of males of similar age who were reared under the conditions usually employed for cockerels.

Material and Methods

All the birds used in this study were Brown Leghorns derived from a control line kept at this laboratory. All the males were hatched in single boxes and four of them were then removed and brooded under conditions in which they were unable to see one another or any other bird. Similar conditions were maintained after brooding. The ten control birds were brooded with other birds and then at eight weeks of age were placed in a pen together where they remained until six months old. They were then put into single cages and were thus kept during the course of the mating trials which were started when they were six and a half months old, the approximate age at which cockerels are usually taken from the all male flocks and mated.

For the mating trials two pens of sexually experienced pullets were used. Each cock was released singly in a pen in the late afternoon and observed for ten minutes by the author who was hidden. The order of release of the isolated and control birds was randomised and, prior to the start of the mating trials, the isolated males were given several hours each day in an empty pen, where they could see no other birds, in order that they could become acquainted with free movement and other conditions in the trial pens. The control birds were observed for several hours each week during their stay in their communal pen to ascertain their peck order positions.

The Mating Trials and Other Observations

In order to test whether young males would respond to a dummy, a stuffed Brown Leghorn pullet in the crouching, i.e. sexually receptive, position was introduced into the control pen when the cocks were fourteen weeks old. The males, 3, 4, 7 and 8 attempted to tread it, but as there was much jostling, none succeeded in completing the copulatory act. This was their only hetero-sexual experience. Some homosexuality was observed; No. 3 mounted several birds and No. 2 attempted to do so, but being

Table I. The Type of Behaviour Shown by each Cock during the Mating Trials, which are shown in Chronological Order.

	Cock	Total no. of matings	Trial 1	Trial 2	Trial 3	Trial 4	Trial 5	Trial 6	Trial 7	Trial 8
Control males	1	43	*Normal	Normal	Normal	Normal	Normal	Normal	Normal	Normal
	2	43	*Normal	Normal	Normal	Normal	Normal	Normal	Normal	Normal
	3	38	*Normal	Normal	Normal	Normal	Normal	Normal	Normal	Normal
	4	22	Aggressive	Aggressive	*Aggressive	Normal	Normal	Normal	Normal	Normal
	5	17	Aggressive	*Normal	Normal	Normal	Normal	Normal	Normal	Normal
	6	15	Aggressive	Aggressive	*Aggressive	Aggressive	Normal	Normal	Normal	Normal
	7	0	Aggressive	Aggressive	Aggressive	Aggressive	Aggressive	Aggressive	Aggressive	Aggressive
	8	0	Aggressive	Aggressive	Aggressive	Aggressive	Aggressive	Aggressive	Aggressive	Aggressive
	9	0	Aggressive	Aggressive	Aggressive	Aggressive	Aggressive	No notice of ♀♀	No notice of ♀♀	No notice of ♀♀
	10	1	Aggressive	Aggressive	*Aggressive	Aggressive	Aggressive	Aggressive	Aggressive	Aggressive
"Isolated" males	I_1	22	Normal	Normal	*Normal	Normal	Normal	Normal	Normal	Normal
	I_2	5	Aggressive	Aggressive	Aggressive	Some normal display	Some normal display	*Aggressive	Normal	Aggressive
	I_3	0	Aggressive	Aggressive	Aggressive	Aggressive	Aggressive	Aggressive	Aggressive	Aggressive
	I_4	0	Aggressive	Aggressive	Aggressive	Aggressive	Aggressive	Aggressive	Aggressive	Aggressive

*indicates when the first mating took place.

low in the social order he was usually repulsed.

In Table I is shown the number of the mating trial in which the first mating, attempted or completed, occurred. Also given is the number of such matings performed by each male in the two pens. The males from the control group can be divided arbitrarily into three classes: those that mated during their first trial run; those that mated at some time during the eight trials and those that did not mate at all during the eight trials. The "isolated" males can be divided equally between the last two classes. The bird No. 10 showed exceptional behaviour in that he performed one incomplete mating during his third trial, and did not mate again.

The normal courtship of the sexually experienced cock has been described (Wood-Gush, 1954, 1956) and the normal courtship mentioned here follows the pattern described in these earlier papers; the aggressive behaviour recorded here means either an attack by the cock on the hens with his spurs or a threat posture by the male which was identical with the fighting stance sometimes adopted by a cock prior to a fight with another cock. Those cocks that mated quickly with the hens showed normal courtship behaviour and in most other cases the cocks behaved aggressively until they mated when aggressive behaviour declined. If no matings occurred aggressive behaviour continued throughout the eight mating trials. In some cases the switch from aggressive behaviour to normal behaviour does not coincide exactly with the occurrence of the first mating, but the trend appears to be fairly general and consistent. A nice contrast in the behaviour of some cocks to live females and dummies is shown by the cocks 4, 7 and 8, who tried to mount the dummy hen but acted aggressively towards the live females for varying lengths of time. It must be added that the hens at the start of each mating trial treated all cocks alike but after any active aggression by a cock they tended to keep away from him.

After the first series of trials a pullet in full lay was placed in the cage of each of the males that had not copulated, i.e. Nos. 7, 8, 9, I_3 and I_4 and also 10. They were left there for one

week and then removed. The cocks were then given another two mating trials similar to the previous ones. Four males that had mated were used as controls; No. 1 and 2 that had the highest scores and Nos. 5 and 6 that had the lowest scores among the males that copulated in the first set of mating trials. The results are shown below in Table II.

Table II. The Second Series of Mating Trials, after each Experimental Bird has had a Laying Hen in its Cage for One Week

	Number of matings		
Cock	Pen 1	Pen 2	Total
8	3	4	7
10	2	2	4
7	0	0	0
9	0	0	0
I_3	0	0	0
I_4	0	0	0
1	5	5	10
2	5	4	9
5	4	3	7
6	2	2	4

In this series Nos. 8 and 10 now courted and mated normally. After this series of mating trials the four cocks which still had not mated were placed in cages next to four control males with high sex drive scores, viz. Nos. 1, 2, 3 and 4. Each male could then see the activities of the other birds and a pullet was placed with each of the eight cocks. After one week the females were removed and the males I_3, I_4, 7, and 9 were again given two mating trials. The birds I_3 and I_4 mated and courted normally while No. 7 behaved aggressively in both trials but mated in the second trial. No. 9, however, did not mate but continued to act aggressively.

Discussion

The actions of the young cockerels, when exposed together to the dummy pullet, indicate that the crouching hen provides a mating stimulus of very high valency. The later results, however, show that with some cocks a certain amount of adjustment is necessary before normal courtship and successful mating can occur. The common sequence of aggressive behaviour followed by sexual behaviour in both control and isolated groups of birds suggests that many males have come to realise that the hens are sexual partners and not merely competitors for food and space. In those cases where the libido is relatively strong, as measured by mating frequency, it is probable that the mating responses are released by a wider variety of stimuli, e.g. Nos. 2 and 3 that had high scores for mating activity were also homosexual in the male pen. The course of adjustment of a male with a medium or low sexual score might resemble the following simplified description. On the release of the male into the pen some of the hens approach him, then he attacks them and some crouch momentarily before fleeing. The male, left alone, tidbits and this may attract one or two hens to him; one may crouch on approaching the cock, who then attacks. Thus, in the course of time the cockerel receives many crouches, for there was evidence in this work of some hens always crouching to the males. Eventually, if the stimulus of the hen's crouching was additive in effect, the libido of the male would be gradually activated until it found expression, and the aggressive drive would then be curbed as in the normal courtship display.

This relationship between the aggressive and mating behaviour of the sexually inexperienced males may, from the data available, be due to one of two causes. Firstly, the aggressive drive may mask the sexual drive until it has been sufficiently activated by repeated exposure to females. Secondly, the aggressive behaviour of the cocks may be aroused not in competition with the sex drive but because other drives are absent or only weakly activated. It is impossible from the present data to say which of these two suggestions is the better. Wood-Gush (1957) showed that in males with some sexual experience there was no correlation between the relative strengths of the aggressive and sexual drives when the measurement of each drive was obtained from a relative measurement from a number of males. Therefore if the aggressive drive does actually mask the sex drive of the inexperienced cock, the period of adjustment would depend on the strength of the two drives relative to one another.

The means whereby the males that were caged opposite sexually experienced males became adjusted should provide an interesting

study, for it is highly probable that social facilitation was involved, and it seems likely that it was also involved when the young cockerels as a group tried to copulate with the dummy pullet, for two of the males that were foremost in this action took a relatively long time to adjust themselves to live hens.

The behaviour of bird I_1 indicates that if the sex drive is strong enough, normal courtship can occur without previous social experience. The general similarity in behaviour between the control birds and isolated birds really questions the efficacy of the common method of rearing males. In this way they are isolated from females when 6-8 weeks old until the age of 6½ months. Normal mating behaviour may be found in cockerels by 80 days of age (Wood-Gush, 1957) and so possibly many males may suffer repression during the isolation of the sexes, and in some the strength of the sex drive may actually be diminished. Although Guhl, *et al.* (1945) showed that competition between adult males may lead to extinction of the mating responses in some cocks, the evidence from this work indicates that social facilitation may be important in enhancing the sexual behaviour of young males. It is intended that these points will be investigated in the near future, for under practical conditions poor fertility is often found for some time in pens where new and sexually inexperienced cockerels have been introduced, and the data presented here may help to account for this phenomenon.

Summary

Four Brown Leghorn males were reared and kept in isolation until the age of 6½ months when their individual behaviour with females was compared to that of ten males which had been reared in the usual way.

No clear-cut difference was found between the behaviour of the two groups towards females. In both there were males that courted the females normally from the beginning and males that at first behaved aggressively towards the females. In these cases the length of time taken for normal courtship to replace aggressive behaviour varied between males. In general, it appears that the cockerels with the higher sex drives, as measured by mating frequency, adjust themselves more quickly than the other males, and possibly respond to a wider variety of stimuli.

The results of exposing young males to a dummy pullet and data from other sources, suggest that social facilitation may play an important role in the adjustment of some cockerels.

The present methods of rearing cockerels under practical conditions are questioned and discussed.

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THRESHOLD FOR ELECTRIC SHOCK OF THE LABORATORY RAT

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Introduction

When obtaining data to establish a sensory threshold a difficulty arises if the experimenter is working with animals. Not being able to use verbal means to communicate the nature of the task he is obliged to condition his S to respond differentially to different values of the dimension he is exploring. In Pavlov's classical studies, for instance, the dog is trained to respond differentially to a circle and an ellipse. As the ratio between the axes of the ellipse is gradually reduced a point is reached where the discrimination can no longer be maintained and behaviour becomes disorganised. Because of this "neurotic" behaviour it is impossible to study discrimination processes throughout the region of uncertainty. The threshold, usually defined as that difference which is detected, or responded to correctly, at a level 50 per cent. above chance, is approached but never established.

With a human S it is possible to pass through this region of uncertainty and obtain a normal ogive of response probabilities from which the threshold may be derived directly.

Several attempts have been made to develop a technique which will give comparable data using animals, but all are open to criticism. Since there is a number of studies on the auditory threshold of the rat the two most adequate of these will be considered and their defects discussed.

The first of these earlier techniques is that used by Gould & Morgan (1942). The rat was placed on a grid, an audible tone was sounded, followed by an electric shock from which the animal escaped by moving to another part of the box. After a while avoidance conditioning was established and the rat moved upon hearing the tone, no longer receiving the shock. The intensity of the tone was then gradually reduced from one block of trials to the next until the rat began to fail to avoid the shock.

The experimenters rightly perceived that if they were to continue in this fashion the habit would break down entirely since the rat would be faced with an insoluble problem. To avoid this they were obliged to adopt the somewhat arbitrary criterion that when the rat failed to respond to 30 per cent. or more of the stimuli in a block of trials no further shocks would be given in blocks of trials using lower values of the stimuli.

This in effect meant that the experimenters had no means of knowing at what level the habit, as distinct from the number of responses, was being maintained at these lower levels of auditory stimulation. To make this distinction clear; under no-shock conditions there was no way of knowing whether or not and how often the rat (*a*) made a "chance" response without hearing the stimulus, or (*b*) heard the stimulus and failed to make a response. The assumption was that since the rat had been responding 100 per cent. correctly at values well above the threshold it would continue to maintain the perfect habit of lower values.

This is precisely the assumption that we cannot afford to make. During these trials at lower values of the stimuli the animal is being deprived of the only criterion available with which to validate a discrimination between stimulus and no-stimulus. Put another way, the animal has learned to discriminate between loud noise and no noise using shock as a criterion of success, but it is deprived of the opportunity to learn to discriminate between little noise and no noise, because there is no outside criterion against which to validate attempts at discrimination. Had training continued at, say, the 90 per cent. successful level there is good reason to believe that the performance would have improved considerably and the final threshold would therefore be lower. Both the evidence from the next experiment to be considered and the present study support this view.

Cowles & Pennington (1943) used a classical conditioning procedure to attack the same problem. The unconditioned response of the rat to a shock applied to its tail was to squeak. This response was conditioned to a tone preceding the shock. Under these conditions lower values for the rat's auditory threshold were obtained than by Gould & Morgan.

But still the technique is unsatisfactory for

two reasons. In the first place squeaking is not as clear-cut a criterion as we should wish. There must be occasions, particularly around the threshold, upon which it is difficult to decide whether or not the animal did squeak. Both the experimenter's own threshold and his proneness to the "stimulus error", i.e. his tendency to perceive in terms of what he expects to perceive, will make the results unreliable. These difficulties could be overcome in principle by use of a recording instrument, but this still leaves us with the second objection which is more fundamental.

In recent years evidence has been accumulating which suggests that at threshold intensities there is a sense in which a stimulus may be both perceived and not perceived. *Vide* Singer (1956) for a summary of the recent literature.

Without entering into the metaphysics of "sub-ception" it is clear that a threshold is only meaningful relative to some specific response, and in general it would seem the less "voluntary" the response the lower the corresponding threshold. The squeaking used as a criterion by Cowles & Pennington comes nearer to an involuntary reflex than a choice judgment. There is therefore reason to suppose that the thresholds they obtained were lower than would be expected relative to a discrimination habit in a "free choice" situation such as is generally understood when defining a threshold and in fact used when obtaining thresholds with human Ss.

The present study is concerned, not with auditory thresholds, but with thresholds for electric shock. Apart from a study by Dunlap (1931) which gives 40 micro-amps as detectable, but states no criterion, the only other experiment to be found on this topic is that of Muenzinger & Mize (1933) in which "sudden movement" was adopted as a criterion of detection and the 30 per cent. level of response as the threshold. Under these conditions 77 micro-amps was offered as the sought value. Ignoring the use of the 30 per cent. correct level as against the common practice, it seems highly unsatisfactory to use "sudden movements" as a criterion, since it is fairly obvious that the animal may well detect shocks of a far lower intensity in the sense of being able to respond differentially to them, and still not be stimulated sufficiently to evoke a "sudden movement."

More recently it has become customary to distinguish between the cue value and drive value of a stimulus, Dollard & Miller (1950), and it is probable that the value obtained by Muenzinger & Mize is more nearly related to the drive threshold than to the cue threshold. Since shock is used so extensively in experiments with rats it is strange that we are still ignorant of the level at which shock may be used simply as a cue, and what conditions affect this level. As was clearly recognised by Muenzinger, Forbes & Wendt (1935) since electric shock is used so widely in experiments with rats some standards need to be developed. This almost inevitably entails the establishment of a threshold and knowledge of factors influencing it.

The first attempt by the author to establish this datum ran into the difficulty previously discussed. The rat was faced with two alleys, one or other of which was electrified on each trial, food being available at the end of the no-shock alley. Choosing the shock alley resulted in no food, the rat being trapped.

The habit was learned readily enough and the shock then steadily reduced. When the discrimination became too difficult, however, the usual "neurotic" pattern appeared; urination, defecation, escape directed hyper-activity followed by immobility and trembling, clawing and biting of the experimenter when picked up. Rest periods of a few days followed by retraining on high drive with well above threshold stimuli restored the habit and finally reduced the threshold to below the earlier level.

Using this technique one animal ultimately ran successfully on only four micro-amps before the habit again broke down. But it was still impossible to obtain a threshold at the 50 per cent. level because the rat would tolerate no more than a 10 per cent. level of sub-threshold "conflict" trials before refusing to run. To obviate this difficulty the experiment has been redesigned as follows.

Apparatus

This consists in principle of a continuous T maze that is arranged in a vertical plane and functions automatically.

The sections are a starting box, grid, choice point, goal box, and common return alley, arranged as shown in Fig. 1. Valve doors prevent retracing. Each door operates a set of contacts which control the recording unit, food magazine, bolt at choice point, ammonia pump, and level of shock in accordance with the animal's previous responses.

The grid is of the twin electrode type. The floor of the shock compartment consists of two detachable brass surfaces each 1″ wide running

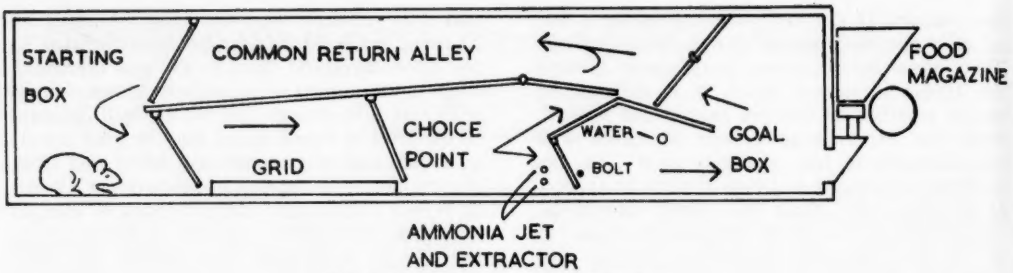

Fig. 1. Elevation of continuous T maze.

along either side, tilted in at 20° to the horizontal with a $\frac{3}{4}$" gap between them. This grid cannot be short-circuited by faeces or urine which simply drop through the gap. Nor can the rat avoid completing the circuit since each electrode is too narrow to permit the animal to put all four paws on it without overbalancing.

The food magazine is of the moving plunger type that delivers about 180 milligrams of ground chow per operation. A thermal flasher is incorporated in the circuit to reduce the risk of non-delivery through jamming.

Procedure

On each trial the rat runs over the grid which may or may not be electrified. If an above threshold shock is present the rat enters the food box and is reinforced. If no shock is present the rat learns to avoid the door to the food box as it remains locked and an attempt to enter produces a whiff of ammonia.

After each trial the rat enters the return alley either from the choice point or goal box and proceeds to the next trial. Under these conditions it learns to accept a 50 per cent. level of positive reinforcement. That is, it receives food on half the trials and avoids ammonia on the remainder.

The 50 per cent. reinforcement schedule is ensured by programming two uniselectors as follows. The trials are divided into blocks of four, on the first two of which the grid carries the level of shock being investigated, which for the sake of convenience we may call the weak shock. If the shock is detected on these trials the grid carries no current for the second two trials. If the shock is detected on neither of the first two trials a shock well above threshold, a strong shock, is provided on the remaining two trials. If the shock is detected on either one of the first two trials the third trial becomes a weak-shock trial. If this is detected the fourth is a no-shock trial; if not detected, a strong-shock trial. In this way the animal gets food on two, and only two, out of every block of four trials.

To reduce guessing, that is, trying the door to the goal box on no-shock trials, ammonia gas is used as a negative reinforcement. On these trials door B remains bolted and any attempt to open it closes a contact operating a valve on an air blower. This results in the air flow being bubbled through a flask of ammonia to a jet immediately in front of the door. The advantages of ammonia as a negative reinforcement when shock is inconvenient are that the animal does not seem to habituate to it, nor is there the danger of audiogenic seizures concomitant with air blast, and its strength is readily regulated. Under these conditions a 10 Normal solution seems to be adequate. Provision for removing the gas shortly after delivery is incorporated.

From the rat's point of view the task is simply one of deciding whether or not the grid is electrified. If the current is present and detectable then an approach response to the goal box produces food. If no current appears to be present then an avoidance response is appropriate since the food is unobtainable and any attempt to reach it only produces ammonia.

Once the discrimination between shock and no shock is firmly established the shock can be reduced to any level without giving the animal an insoluble problem. When a sub-threshold shock is presented the rat simply makes an avoidance response and is thus not deconditioned by finding food on what appears to be a no-shock trial. This trial is compensated for later in the series by the substitution procedure described.

Under these conditions, although hesitation occurs at the choice point for shocks close to the

threshold, no neurotic behaviour is precipitated and the habit is maintained on both sides of the threshold.

Note that it would not be possible to have the animal maintain the opposite habit. If it learned an approach to no-shock the habit would again break down at the threshold, since it would make approach responses for sub-threshold shocks and be punished.

Results

The apparatus being fully automatic it is possible to leave the animal in for several hours per day running an average of one trial per minute. At this stage it becomes clear just how important it is to give the animal an opportunity to learn to use the information available. After about 110 hours and 6,000 trials one animal was responding positively to 20 micro-amps at about the 50 per cent. level. Later on in the same day's running it detected 50 out of 51 stimuli of 10 micro-amps. The following day it detected 37 out of 41 stimuli of 5 micro-amps. Altogether four animals have been run. All were able to detect 20 micro-amps without difficulty, and two were able to detect 10 micro-amps or less.

Discussion

In principle it would be possible for the animal to learn a continuous double-alternation solution. In fact, the rat does not do so, but relies on the shock as a cue. Earlier studies, Hunter (1920), Karn & Patton (1941), have indicated that the continuous temporal double alternation maze is beyond the rat's capacities; a conclusion which is confirmed by the present study where the rat fails to arrive at such a solution after literally thousands of trials.

Due to the way that a constant current circuit of the type described by Muenzinger & Walz (1934) functions, the low thresholds obtained are perfectly explicable. The circuit is arranged so that the voltage of the control grid of a pentode radio valve is related to the rat's resistance in such a way that as the load increases it is compensated for by an increase in the applied voltage.

The qualities of such a circuit are deceptive. It was thought that by applying a constant current the value of the shock was standardised. In fact, what is probably the most relevant variable, the wattage, is left in the rat's control. For by reducing its area of contact with the grid the rat can increase its resistance and the current density, theoretically at least, to infinity. Since the amperage remains constant the voltage increases in direct proportion to the resistance (Ohm's Law), and the wattage, being the product of the amperage and voltage increases likewise.

After some training these rats learned to "sample" minute currents in the following way. Sitting back on its furry rear quarters, which provide effective insulation, the animal places one front paw on one electrode and lightly taps or brushes the opposite pole with its other front paw. Both animals with the very low thresholds were also observed to lick the test paw between successive applications. Once this technique has been perfected it is possible that the applied voltage rises to 300 volts or more for brief periods and the rat is thus able to discriminate these minute currents.

Although a constant wattage circuit is more complex, if the power dissipated is the relevant variable, then it should lead to more reliable results, and work is proceeding on these lines. A study by Hill *et al.* (1952) using human subjects has shown that wattage is correlated significantly more highly with reported intensity of shock than is amperage. Forbes & Bernstein (1935) working with human S's proved that the current required for detection increases logarithmically with the area of the electrode, while the current density needed decreases. They conclude that wattage may well be the right index to use.

Summary

A technique for exploring an animal's ability to discriminate throughout the whole region of the threshold without precipitating neurotic behaviour is described.

Observations and arguments are offered to suggest that the constant current circuits in general use do not in fact control the relevant variable to produce a standardized shock. Because of this it would seem that the detection of minute currents under these conditions is largely an artefact and that the "threshold" is merely a measure of the animal's skill in manipulating the wattage. For this reason any attempt to establish a stable threshold under constant amperage conditions with a variable contact area would seem to be foredoomed.

Earlier estimates of the shock threshold in terms of amperage are certainly much larger than can be obtained under suitable conditions.

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BEHAVIOUR STUDIES ON INBRED MICE: A SELECTED BIBLIOGRAPHY

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This bibliography has been compiled from a much larger one, the Subject-Strain Bibliography, which attempts to include all published papers dealing with specific inbred strains of mice, named genes in mice, or named transplantable tumors. Therefore, the orientation is to the strain of mice rather than to the field of behaviour. However, the author feels that, since research work in behaviour using inbred strains has accelerated sharply during this decade, a selected listing will be of value.

For the purposes of this listing, behaviour is interpreted rather broadly, including reported effects of the neurological mutants but not genetic studies made with these mutants. The list also includes pharmacological studies in which the end point is some activity of the mouse. Mice designated "white," "Swiss," or undesignated are held to be non-inbred. Where a strain has been called inbred but not named, the reference is omitted. Approximately two-thirds of the papers appeared from 1950 on. Literature was searched to the beginning of November, 1957. The author would like to hear of omissions, and to receive reprints of omitted papers, which fall within the selected categories.

Journal references follow the plan of the "World List of Scientific Periodicals." References are listed in chronological order.

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"PUSHING" IN CATTLE: ITS RELATION TO INSTINCTIVE GRASPING IN HUMANS

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It has long been known that domestic ungulates suffering from brain disease sometimes display a pattern of behaviour in which they push their heads repeatedly and persistently against a vertical surface in an apparently meaningless fashion (U.S. Dept. Agriculture, 1904; Dadd, 1891; Hutyra, Marek & Manninger, 1946; McFadyean, 1924). They may push along a fence or wall until they end up with their heads pressed into a corner. A possible significance to this phenomenon was first suggested to us by the fact that some cows with disturbances of the central nervous system associated with postpartum ketosis who showed forceful pushing of the whole body forward against the stanchion (Udall, 1947) also showed pathological sucking and licking with a tendency to grasp objects with their mouth. If the cow is loose, she may push her head against any large obstacle in her path. These effects are reminiscent in many ways of certain reactions of the newborn.

Recent motion picture studies on the nursing behaviour of newborn kids by Blauvelt (1954) and lambs by Moore cast further light on this problem. The newborn finds its mother's teats partly by virtue of an inherent instinctive pattern. The nursling will walk toward any moving object that passes it. The newborn animal will orient along a fence or wall when exposed to an appropriate movement under certain conditions. If an obstacle is placed in its path, it will push against the obstruction. When a person followed by a kid or lamb leaves the room and closes the door behind him, the young animal will continue to walk until it meets the door and then it will edge along the wall and end up with its head pressed into a corner. A maternal contribution to the process of learning to nurse is the dam's desire to lick the amniotic fluid initially covering the kid or lamb. When the nursling first climbs to its feet the following pattern of activity ensues: as the mother approaches the offspring to lick the amniotic fluid, the lamb begins to walk toward its dam which then is usually the nearest moving object. Then the nursling orients along her side. The mother shifts her position as she licks the nursling and correspondingly the young reorients with the movements. A learning pattern of trial and error is established and ultimately the lamb's muzzle is trapped in the ewe's inguinal region. Thus the nursling, like the diseased adult animal, also pushes forward until it ends in a corner; only in this instance the corner is the inguinal region of the dam, from which strategic point it is able to take the next steps in the process of learning to nurse.

Accordingly, it seemed to us that in some adult animals with disturbed cerebral function there is a reappearance of a compulsive pushing pattern which was present as a normal phenomenon in the newborn state but had disappeared with weaning. Moreover, an analogy to normal and disturbed human behaviour also suggested itself to us. In a nursing infant there are grasping hand movements which occur simultaneously with sucking and which match the mouth's activity in their intensity. These movements, like the above-described pushing, are part of a teat-finding manoeuvre. Such associated grasping movements disappear after weaning. However, should brain disease occur resulting in severe impairment of consciousness, the early pattern associated with nursing may reappear even in later life including both pathological sucking and instinctive grasping (Seyffarth & Denny-Brown, 1948).

The incorporation of instinctive grasping and pushing into nursing represents only one use of these patterns. We will now consider another aspect of their utility (Fulton, 1949; Brownlee, 1950, 1954). If one unobtrusively enters a pasture where lactating goats unaccustomed to being approached are grazing with their offspring and where the mothers and young are distributed at random, a wave of panic passes over the young animals as soon as the presence of the human stranger is sensed. Immediately

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each kid runs to is own mother and begins to nurse vigorously. Apparently the return to the mother's teat has an anxiety-alleviating effect on the frightened young animal. Saul Adler (1948) relates that young native children in remote villages in West Africa would also run to their mothers and nurse at the breast when a strange white man appeared. Thus the nursing pattern can be seen to serve a double function. It relates not only to the problem of nutrition but also to the emotional needs of the organism.

Thus, in considering the most primitive problems of adaptation, one finds similarity of behaviour in the representatives of two distantly related orders of mammals. Much has been written about the role of nursing in the emotional development of the human being. Psychoanalytic studies of neurotic patients have shown that fear of leaving home in certain phobics is based on an unconscious need to stay close to mother because of imagined dangers in the outer world (Fenichel, 1945).

One might ask, "Why does the obsolete nursing pattern reappear under certain conditions of disturbed cerebral function?" Let us conceive of the total behaviour of a normal healthy organism as representing a continuous series of successful adaptations to its environment. As the organism develops, new patterns of behaviour are elaborated. In the process earlier modes of adaptation are abandoned. Should more recently acquired behaviour patterns become unavailable as a result of cerebral disturbances, previously repressed patterns may re-emerge, in a manner reminiscent of the psychoanalytic concept of regression.

Summary and Conclusion

It is suggested that the adult animal deprived by cerebral disturbances of its mature adaptive devices displays the primary patterns of its earlier age. In this manner it becomes possible to understand "pushing" in diseased ungulates as an adaptive mechanism analogous to "instinctive grasping" in diseased humans. Both may be associated with pathological sucking reflexes in brain disease, and serve a teat-finding function in the normal nursling. In the healthy newborn and in the brain-injured adult, pushing and instinctive grasping serve an emotionally adaptive function in addition to its primary nutritive one.

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THE MEASUREMENT OF AGGRESSIVENESS IN THE DOMESTIC HEN

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Introduction

Since the recognition of a social dominance hierarchy in the domestic hen (Schjeldrup-Ebbe, 1913) a number of workers (summarised by Guhl, 1953, and Wood Gush, 1955) have contributed to our understanding of the nature of this behaviour pattern and the part it plays in the ecology of the fowl.

In the course of an experiment undertaken to determine the interactions between family genotypes and housing environments (battery cages, intensive and semi-intensive systems), it was realised that differences in the intensity of the "peck-order" would possibly play a large part in determining the reactions of birds in each environment; accordingly, an attempt was made to measure the aggressiveness, as exhibited by pecking, of all birds in this experiment.

Collias (1943) devised a technique for staging encounters between pairs of hens by placing them simultaneously in a neutral pen to settle their dominance relationships: each hen was allowed to meet a number of strange hens and a score was obtained which gave a measure of the relative aggressiveness of the birds tested.

An alternative method might be to divide the number of birds to be tested into a number of small groups and score each bird according to the number of birds in the group it could peck. For work with groups, the ontogenetically developed peck order may be studied or the birds may be isolated in laying eggs and then reassembled.

Guhl (1953) reported correlations between all these methods and also a correlation between repeated paired contest scores of 0.79 ($P=0.01$). He states: "From the foregoing tests to measure relative aggressiveness, one may conclude that there is a tendency for agreement and that any one of the methods might be used to evaluate levels of aggressiveness in a flock. The exceptions encountered do show, however, that more than one of these methods should be used if critical results are desired."

Since any attempt to measure the aggressiveness of large numbers of birds is extremely time-consuming, a preliminary trial using caged birds was carried out to determine which method was likely to give the best results. Birds in the experiment were then scored and the results of this work have been used in an attempt to obtain information on the efficiency of the scoring techniques used and to suggest an improved technique of scoring.

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Material and Methods

Two groups of 12 laying Australorp pullets (panels A and A1) of the same age, and five groups of 10 laying pullets (panels 2-6) were chosen at random within various age groups for the preliminary work. Panels A and A1 were one week older than panel 2 and panels 2-6 each differed in age by two weeks, panel 6 being the youngest. All birds were at least eight months old at the commencement of the work. Panel 1 was then formed by taking the first 10 birds of panel A1.

All panels were run as groups for a short time to determine the peck order which developed and panels 2-6 were then run together as a flock of 50 birds but, due to shortage of time, only 992 of the 1,225 possible pair relationships were determined.

Panels 1-6 were then used for scoring 130 other birds in the same age group, the numbers for each panel ranging between 15 and 25.

All birds in these experiments were housed in laying cages and removed only for the time necessary to settle a single encounter at a time, (or for assembling daily in groups for the determination of peck orders).

The score obtained for each bird was the number of panel birds it could peck and with panels of ten the scores ranged from 0-10.

For rapid identification of birds, the best results were obtained from numbered wing bands of aluminium venetian blind slats $3\frac{1}{2}''$ long drilled for attachment to the wings with cotton tape (Fig. 1).

For paired meetings, birds were placed simultaneously in cages approximately $2\frac{1}{2}' \times 3'$.

Results

Lag Effect of Pecks

Panel A1 (12 birds) was scored against panel A with no time interval between meetings in

Table I. The Results of Panel Grading Without a Time Interval Between Meetings, with Test for Tendency to Runs
Panel A2 used to test the twelve birds of panel A1 (1-12)—all pullets of the same age from cages.

1	2	3	4	5	6	7	8	9	10	11	12
A—	B+	C—	D—	E+	F+	G—	H+	I—	J—	K+	L+
B—	L+	G—	C—	D+	J+	K—	E+	H+	A+	F+	I—
C—	K—	A—	B—	F+	L+	I+	D+	G+	H+	J+	E—
D+	F—	I—	A—	L+	E+	C—	G+	J+	B+	H+	K+
E+	D—	F—	G+	J—	K+	A—	L+	C+	I+	B+	J+
F+	H—	K—	E—	G+	C+	D+	B+	A+	L+	I+	J+
G+	I—	D+	F+	K+	H—	J—	A—	L+	C+	E+	B+
H—	E—	L+	J+	C+	A—	B—	I+	K+	D+	G+	F—
I—	J—	B—	L+	H+	G+	F—	K+	D+	E+	A—	C—
J—	C—	E+	K+	A+	I+	H—	F+	D+	G+	L+	D+
K—	G—	J+	H+	I+	B+	L—	C+	E—	F+	D+	A—
L+	A—	H+	I+	B+	D+	E—	J+	F+	K+	C+	G+
5	2	5	7	11	10	2	11	10	11	11	7
3—	2+	6—	4—	4+	6+	2—	6+	1—	1—	8+	1+
4+	10—	2+	1+	1—	2—	1+	1—	9+	11+	1—	2—
4—		1—	1—	7+	4+	2—	5+	1—		3+	4+
1+		3+	6+			1+		1+			2—
						6—					1+
											1—
											1+
P0.076	0.030	0.076	0.076	—	0.18	0.45	—	0.45	0.2	—	0.65 (more runs)

Chi^2 (18df) = 32.979. P=<0.02

latin square random order. There was a significant tendency ($P<0.02$) for birds which had been pecked once to lose in their next encounter and for those which had pecked once to win again in their next meeting (Table I). The test for runs was that of Swed & Eisenhart (1943).

Repeatability of Score Against the Same Panel

After a month this work was repeated twice at four-weekly intervals using the same two panels of 12 birds and providing a break of at least three hours between meetings. This data showed no evidence of any tendency towards runs.

The repeatabilities of score of panel A1 against A and A against A1, as measured by regression (which shows coincidence as well as concordance), of second scores on first scores were 1.06 (P 0.001) and 0.905 (P 0.001). (Correlation coefficients were 0.912 and 0.845 respectively.)

These regression coefficients indicate that scores obtained against a panel are highly repeatable after an interval which should have been quite adequate to prevent birds, which had only met once previously, from remembering each other (Schjelderup-Ebbe, 1923).

Score in Small Groups

Panel A was assembled daily as a group until the peck order had been determined twice at more than eight weeks interval. Score in a small group was measured by the number of birds pecked so that in a group of 12 birds scores ranged from zero to 11.

The regression coefficient giving the repeatability of the scores obtained for each bird was 0.809 (P=0.001).

PLATE III

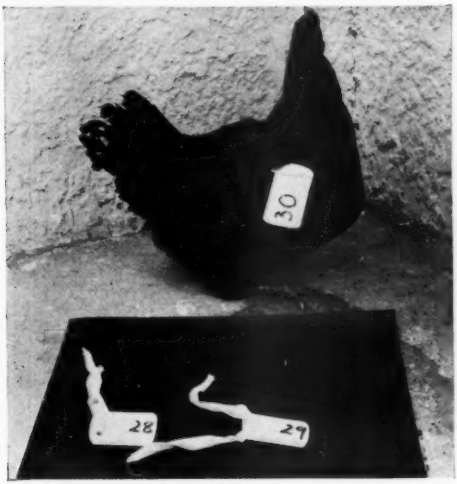

Fig. 1. Wing bands used for rapid identification.

Table II. Repeatability of Panel Score Against Two Different Panels

Panel	Size of 2 random groups met	Range of scores Gr. 1	Gr. 2	Regression coefficient	Correlation coefficient	P
1	12	1–11	2–11	0·709	0·841	0·01—0·001
2	7	0–3	0–2	0·067	0·090	N
3	10	4–9	4–8	0·318	0·298	N
4	10	2–9	0–9	0·950	0·858	0·01—0·001
5	10	0–10	2–10	0·834	0·901	0·001
6	8	4–7	3–8	0·900	0·669	0·02—0·05

Repeatability of Panel Score with Time Interval against Two Different Panels

Since panels 1-6 were used to score between 15 and 25 birds each, these panels can be said to be scored against these larger groups of birds; the complete control over conditions of meeting make the use of scores in each direction valid. The birds met by each panel were divided to form two randomly-chosen groups of size 7-12. Thus, the birds in each panel had two scores against groups of birds chosen at random: an estimate could then be made of the regression of score against one group on score against the other. The results are given in Table II.

The Relationship between Scores Obtained in an Assembled Small Group and Scores against a panel with time Interval

The results are shown in Table III.

Large Group Rankings and Their Relationships to Other Scores

Although all relationships were not obtained when panels 2-6 were run as a group of 50, all relationships within 3 panels (3, 5 and 6) were obtained under large group conditions. These were related to the scores which were obtained previously when these panels were run as small flocks and also to the panel type scores which birds of these panels obtained later (used in Table III). A series of non-significant regressions ranging from 0.217 to 1.06 was obtained.

The Effect of Small Differences in Age on Scores Obtained in a Large Group

On the incomplete scores obtained in the large group there was no relationship between score and age over the small range of ages studied (ten weeks).

Discussion and Conclusions

These results show that, because of the lag effect of an encounter, it is impractical to use a single panel when a large number of birds are to be scored for aggressiveness. They suggest further that, though the repeatability of scores obtained in small flocks is not significantly lower than the repeatability obtained with

Table III. Regression of Score in Small Group on Panel Score

Panel	No. in panel	Regression coefficient	P
A1	2 x 12	0·828, 0·794	0·02–0·05, 0·01–0·001
A	12	0·641	0·05 – 0·1N
2	10	1·736	0·01
3	2 x 10	0·1776, 0·45	N, N
4	2 x 10	1·0, 0·578	0·01–0·001, 0·05–0·1 N
5	2 x 10	0·330, 0·428	N, N
6	10	0·838	N

scores against panels, because of the peck lag effect there is reason to believe that the score against a panel is a more efficient measure of aggressiveness. Observations on newly-assembled flocks showed a high intensity of pecking which provided conditions under which the peck lag effect could interfere to some extent with the peck order obtained.

If birds are to be scored against panels, and the high repeatability of panel score suggests that this is desirable, more than one panel is needed. There are a number of problems associated with the choice of panels and the conversion of results obtained on different panels to a single, relative scale. The results obtained when birds are scored against different randomly-selected panels (Table II) show that when the range of scores obtained is adequate, the scores on different panels show a high relationship.

The fact that two such tests out of 6 gave quite unsatisfactory regression coefficients suggests that birds to be incorporated in panels should not be chosen at random. The following approach is suggested.

The Number of Panels Needed

In the present case six were chosen. It was estimated that up to 120 meetings per day could be observed, so allowing each panel bird to be used twice. However, under Queensland spring and summer conditions, the best figure realised was 85 meetings on a relatively cool day, with an average of 50-60. More pecks were observed in the morning than in the afternoon.

Size of Panels

The present rather limited evidence suggests that ten birds can be quite adequate.

Choice of Panel Birds

It is suggested that a number of the birds from which panels are to be chosen, should be scored against a single calibration panel. The number of birds scored should be in excess of that required for the panels. Preliminary tests would be necessary to choose an adequate calibration panel although bodyweight and comb size may be used as a guide (Collias, 1943).

From the birds scored, panels may be chosen, grouping individuals so that there is an adequate range of scores in each panel. Birds may then be tested against the panels so formed and the scores converted into scores against the calibration panel.

Since high regressions can be obtained between scores made against two different randomly-selected panels when the range of scores are adequate, the errors involved in such a conversion are likely to be low.

The variable relationship shown between scores in small flocks and scores against panels may be due to the fact that the conditions of scoring were completely different: the peck lag effect may play a part in this. An alternative explanation may be the fact that under flock conditions, each bird is scored against a slightly different assembly of its fellows.

The fact that panel 2 gave a significant regression coefficient is surprising in view of the small range of scores it obtained against a panel of 10 (0-4).

It is probable that under large group conditions, the peck lag effect demonstrated above would play a much more important part than it would under small group conditions since when this group was assembled daily, the rate of pecking was of a high level, requiring at least two observers and two recorders.

Summary

1. An attempt has been made to find an adequate method of measuring aggressiveness in large numbers of birds by scoring against standard panels of birds under controlled conditions.

2. A peck lag effect has been demonstrated; this means that the use of such panels requires that an interval of time elapse between successive encounters of any bird.

3. The panel scores obtained have been shown to be highly repeatable.

4. When a number of birds are scored against two randomly-chosen panels the repeatability of score is high when the panels show a wide range of scores.

5. To score large numbers of birds when a time interval is necessary between encounters, it seems desirable that a number of birds suitable for inclusion in several panels is first calibrated against a standard panel. The score of each bird is determined and panels, each showing a wide range of scores, should then be selected. The scores made against these panels are then converted into scores against the calibration panel.

6. Small differences in age of birds appeared to have no relationship with aggressiveness in large groups.

7. The regression of score in a small group of initially strange birds on panel score have been shown to be variable: less than half showed statistical significance.

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THE DEVELOPMENT OF SOCIAL ORGANISATION IN THE DOMESTIC CHICK*

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The social behaviour of adult chickens has been investigated extensively. Reviews of behaviour studies (Wood-Gush, 1955) and of social behaviour in particular (Guhl, 1953) of these birds have shown that little is known about the development of behaviour patterns in domestic chicks, especially agonistic behaviour and the establishment of the initial peck-order. Noble & Zitrin (1942) experimented with sex hormones to induce precocious sexual behaviour. Collias (1950b) with somewhat similar treatment observed both sexual behaviour and aggressiveness. Smith (1957) found evidence of social "learning" in domestic chicks. Observations on the early socialisation of chicks (Collias, 1952) were not carried to the stage of peck-order formation. Wood-Gush (1957) noted some stages in the development of agonistic behaviour in chicks prior to the establishment of what he called the ontogenetic peck-order. However, he was primarily interested in the probable correlation between levels of aggressiveness and sexual activity.

The objectives of the study required some initial observations and a series of subsequent experiments. Information was needed on the various behaviour patterns; the sequence in which these appeared; and the age at which the initial peck-order developed. Sex hormones are known to influence social behaviour patterns in adults (Allee, Collias & Lutherman, 1939; Allee & Collias, 1940) and in chicks (Collias, 1950b). Could exogenous androgen and oestrogen affect the sequence in which behaviour patterns develop or the age at which dominance relations become established? Would castration cause any deviations from the normal development of social behaviour and organisation? Do these hormones have similar inductive effects in both sexes? Experiments were also devised to give some information on the psychological aspects of developing social behaviour. Organised pecking as evidenced by dominance-subordination relations involves learning or conditioning. Does rearing in partial isolation alter the age at which the social order may be established? Of interest here are the effects of early inter-individual contacts on the later establishment of peck-rights, and the effects of certain habits (as the reinforcement which constitutes social inertia) on the evocation of behaviour patterns and social organisation. Finally, the results presented an opportunity to relate them to certain ontogenetic phenomena and concepts of inherent behaviour.

*Contribution Number 285 from the Kansas Agricultural Experiment Station in the Department of Zoology; and Number 322 from the Department of Zoology.

Methods

Chicks were obtained from the Department of Poultry Husbandry and from a commercial hatchery. The former were received on the day of hatching and the latter on the day after hatching. One set of chicks, White Rock males, was four weeks old when received. Experiments included two strains of White Leghorns; one strain of White Rocks; and commercial hybrids. Samples of these strains and/or breeds were small and the results may not be typical of their populations. Availability determined the various breeds or strains used.

All experiments were conducted in a basement laboratory in Fairchild Hall. Ventilation was provided by two exhaust fans. During brooding and to about five weeks of age the chicks received 24 hours of light daily, thereafter a period of 12 hours of light was regulated by a time switch. This laboratory was steam heated during the winter months. The experiments were conducted during various seasons and over several years.

The equipment used to rear the birds varied and no experiments were made to determine whether such differences influenced the development of behaviour. Attempts were made to keep physical factors (temperature, hours of light, and floor space per bird) similar for group-reared and isolated chicks within each experiment. Three methods of brooding were used. The order in which they are described is the same as that in the presentation of the results. The heterosexual flocks and the White Leghorn males were started in a large brooder measuring (inside dimensions) 66 × 33 × 9 inches; the

heating compartment was 24 × 33 inches. The area was partitioned as needed for groups of chicks and isolated chicks (cell areas were 28 × 4 inches with six inches extending under the heating compartment). The White Leghorn females were brooded on the floor in pens and heated with infra-red lamps. This arrangement facilitated observations. The chicks in partial isolation were in a floor cage constructed of half-inch mesh screening with cells 24 × 11 × 10 inches, and 25-watt lamps in the cells to furnish heat and light. The hybrid chicks in the capon experiment were brooded in five small (20 × 18 × 6 inches) brooders with wire floors and heated with a 25-watt lamp. The time at which chicks were moved from brooders to floor pens varied from three to six weeks of age. The floor pens had an approximate area of 8 × 7 feet.

The partially isolated chicks used in the experiments concerned with the assembly of chicks at various ages were reared in cages composed of cells. Two sizes were used. The smaller cells used during brooding were 10-inch cubes. The half-inch mesh partitions were arranged to give each chick two neighbours, and were heated with a 25-watt lamp. As the birds grew they were moved to cages with cells measuring 15 × 13 × 15 inches, in a similar arrangement. The outer walls of this cage were made of 2 × 3 inch welded wire, and troughs for food and water were suspended on the outside of these cages. Attempts by chicks to peck each other through the screen were unusual. The isolated chicks were assembled by removing the partitions. The group-reared controls of these experiments were brooded in the large brooder described above and then placed into cages having a unit floor area per bird which equalled that of the isolated birds. The final experiment on social inertia used these cages with or without the partitions as needed.

Within each experiment the chicks were distributed among cages at random. Upon receipt each chick was wingbanded as it was taken from the shipping boxes, marked with a colour(s) for rapid identification, and placed into a brooder, cage, or cell for isolation. The placements followed an order until there were equal numbers (usually ten) in each group. The dyes were dissolved in 70 per cent. alcohol, which gave fairly rapid drying, and painted on the down of backs or wings. Re-application of colours was necessary as the feathers developed. The individuals are indicated in the tables by letters representing the color(s) used.

The androgen used in some of these tests was testosterone propionate (Oreton*), and injected daily into breast muscles with the alternation of right and left sides. The oestrogen was a suspension of diethyl-estradiol (Jen-Sol†) which was injected every other day. All birds which received exogenous gonadal hormones, and all the capons, were autopsied at the end of each experiment to verify the sex or, with capons, to determine macroscopically whether any portions of testes were present.

Observations were made by the author and four different students who varied much in their training and experience with chickens. To keep subjective differences in the interpretation of a peck or threat at a minimum, it was agreed to record delivered pecks and to consider undelivered pecks as threats. Variables, in addition to those of probable genetic origin, may have been introduced by subjective differences in recording. However, the results were in basic agreement within certain limits.

The Development of Some Behaviour Patterns

The prehatching and posthatching behaviour of domestic chicks were reviewed by Wood-Gush (1955) and discussed by Collias (1952). This report is concerned particularly with the developmental sequence of certain behaviour patterns which lead to social organisation. Behaviour patterns may be considered as social if they are either "contagious" (or social facilitated behaviour, Armstrong, 1947) or lead to inter-individual activity. The order in which they tended to appear was: escape (fear) reactions, frolicking, sparring, aggressive pecking, avoidance and fighting.

The escape reaction was common after the third day posthatch, and could be readily elicited by any object moving above the chicks. Some chicks responded sooner than others and all soon dashed about the brooder frantically. Such reactions appear at a much later age in birds which are fed in the nest, e.g. passerines (Nice, 1943, p. 52). During the first week of age chicks began to frolic, a spontaneous activity in which individuals ran briefly with wings raised. Such activity by one often induced others to frolic although not necessarily in the same direction. By the second week frolicking lead

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†From Jensen-Salsbery Laboratory, Kansas City, Mo.

to sparring, Two chicks, after frolicking, jumped up and down, as adults do when fighting, but the chicks failed to deliver any blows with their beaks. The activity waned readily and the partners pursued other activities. The earliest aggressive peck was noted late in the second week. However, this behaviour was quite unusual at this early age. Avoidance of another chick in response to aggressive action was indicated during the fifth week, although a given chick did not habitually avoid certain others at this time. A chick would move away when pecked but might at times return to peck its aggressor. Fighting was observed as early as the sixth week, but usually ended without any decision.

Dominance-subordination relationships, or peck-rights, developed later, presumably when aggressive attacks were more intense and when individuals could be recognised and thereby avoided as individuals. Attempts to determine the age at which recognition of penmates developed were unsuccessful. The peck-order is the best evidence for recognition of individuals (Guhl & Ortman, 1953). Tests made with strange chicks (not members of the same group) were not conclusive. The introduction of younger chicks however elicited threatening stances or pecks as early as 10 days of age, but such chicks were dissimilar in appearance, size, and probably in behaviour, from penmates. Smith (1957) has presented some evidence that Leghorns of ten days of age would discriminate partners of the same breed but from a different flock.

In the sequence of development there was much variability between individuals and groups with regard to the age at which these behaviour patterns became evident. There was also much overlapping in the sequence. Presumably there was variability in rates of development, but there were also indications that the intensity of stimuli (external and/or internal) varied. Frolicking, sparring, or fighting occurred more often subsequent to turning on room lights, or at feeding time, but soon subsided. The chicks appeared to be well adjusted to a given behaviour level in development, and data were slow in accumulation. New patterns appeared rather abruptly and soon subsided with readjustment. These observations suggest what Kortlandt (1955) called "ruptural behaviour."

Differences Between Male and Female Chicks

The initial observations were made on groups of chicks, the sex of which remained unknown until sexual dimorphism developed. These White Leghorn chicks (Kansas State College strain) were divided at random into two groups of 18 and 19. Observations began on the day after hatching and continued, for some of them, for 21 weeks.

Aggressive approaches and delivered pecks were recorded separately during the early weeks and also as to which chick pecked and which received the peck. No aggressive action was seen during the first week. After it was possible to determine the sex of the individuals the data were summarised (end of six weeks) as to unisexual and heterosexual pecking. This was of interest because adult males usually do not peck the hens nor are they pecked by them. An effort was made to note the age at which a pecking dichotomy would appear.

The aggressive actions recorded during the first six weeks are summarised in Table I. The cockerels (males) were more aggressive than the pullets (females). A total of 118 pecks by males on both sexes were observed, whereas the pullets pecked only 13 times during the same length of time. Only 36 of the pecks by males were delivered, and only 4 by the females. The pecking at this age was infrequent and of low intensity. There were about twice as many aggressions observed in group 9C as in 9D (88 to 43). This variable was related to the sex ratio. Group 9C contained 10 males and 8

Table I. Peck-like Aggressive Approaches and Delivered Pecks Observed during the Second and through the Sixth Week; no Aggressions were noted during the First Week of Age

Interactions	Groups*	Peck-like action	Delivered pecks	Total
Male on male	9C	46	16	62
	9D	11	9	20
Male on female	9C	12	9	21
	9D	13	2	15
Total by males		82	36	118
Female on male	9C	2	2	4
	9D	4	1	5
Female on female	9C	0	1	1
	9D	3	0	3
Total by females		9	4	13

*Group 9C composed of 10 males and 8 females. Group 9D composed of 8 males and 11 females.

females, and the 9D group had 8 males and 11 females. Most of the aggressive actions were between males; of the 118 actions by cockerels, 82 were on males and 36 on pullets. The pullets pecked cockerels more often than they pecked females, but the data are too few to be taken seriously. One may conclude that these figures indicate a partial dichotomy in social organisation at the onset of agonistic behaviour.

The chicks were moved from the brooder to floor pens at the end of the sixth week. Similar data for weeks 7 through 15 are given in Figure 1 as percentages of pecks delivered by members of each sex in group 9C. The periods of observation were not of uniform duration and rates of pecking could not be given. The curves in the figure are based on a total of 4,210 pecks, of which 3,585 were delivered by ten cockerels and 625 by eight pullets. Only 25 of the pullet's pecks were on males, but 637 were delivered by cockerels on the females. The figure shows that heterosexual pecking diminished gradually. The results from group 9D were quite similar, but with less heterosexual pecking during the seventh week.

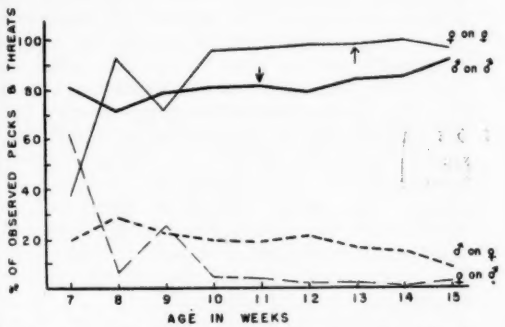

Fig. 1. The gradual development of unisexual pecking is shown by the percentage of unisexual and heterosexual pecking which occurred during the establishment and the maturation of peck-orders. Arrows indicate the time at which peck-orders were formed in group 9C

The cockerels began to show sexual behaviour during the eighth week, but this behaviour did not become intense until the 15th week as did dominance behaviour. The pullets were definitely under social stress in both groups and had comparatively little opportunity to feed. Most of the cockerels were removed and observations on the pullets were continued to determine when they would develop sexually. The first sexual crouching by pullets was observed during the 18th week, and the first egg was laid during the 21st week.

A peck-order was not established until each individual formed definite dominance-subordination relationships (i.e. obtained the peck-rights over, or consistently avoided) with each of the penmates of its sex (see Guhl, 1953). Tabulations of pecks were made weekly and compared with those of the preceding week. When the pecking relationship between any two individuals became consistently uni-directional then dominance was considered as established for that pair. Tables II and III show the ages at which various peck-rights were established for each individual. The letters under the column "peck-order" represent the colour(s) used to identify each individual. In this column each chick pecked those listed below it unless an arrow shows a deviation from a straight-line peck-order.

On examination of Tables II and III it will be noted that the males began to establish dominance somewhat earlier than did the females, and that the cockerels also formed a peck-order earlier. A comparison of groups 9C and 9D shows that the 9C individuals began to set up peck-rights earlier than the 9D, and that

Table II. Ages at which Peck-rights were Developed in the Heterosexual Group 9C of White Leghorn Chicks

Number pecked	Peck-order	Weeks of age 6	7	8	9	10	11	12	13
				Normal ♂♂					
8	RR	1	7						
8	BR		4	1	3				
7	RV	1	3	2	1				
7	Y		4	1	1		1		
5	RY		3	1	1				
4	BV	1	1		1	1			
3	B	2		1					
2	BG		1			1			
1	YY			1					
0	G								
45	Total	5	23	7	7	2			
				Normal ♀♀					
7	YV		1	1		3		1	1
6	BY		2	2	2				
5	R			1		3	1		
4	V			1	1		1		1
3	GV					1		2	
2	YG					1		1	
1	RG				1				
0	GG								
28	Total		3	5	4	8	2	4	2

Table III. Ages at which Peck-rights Developed in the Heterosexual Group 9D of White Leghorn Chicks

Number pecked	Peck-order	Weeks of age 6	7	8	9	10	11	12
				Normal ♂♂				
7	BB		4	3				
6	BV			5	1			
5	R		1	3	1			
3	Y			3				
3	RR			2	1			
2	RY				1	1		
2	BR			2				
0	BG							
28	Total		5	18	4	1		
				Normal ♀♀				
10	BY				4	6		
9	G			5	3	1		
8	YG			1	6	1		
6	GV				1	5		
6	RV			1	3	2		
5	GG			1	3	1		
4	YY				1	2		1
3	RG				1	1	1	
3	YV				1	2		
1	V				1			
0	B							
55	Total			8	24	21	1	1

the latter group formed a social organisation sooner. The mean ages at which the males established peck-rights were 7.58 and 8.03 weeks, and for the females they were 9.75 and 9.33 weeks respectively. The males formed dominance relations 2.17 and 1.29 weeks earlier than did the females. Some of the variability probably was due to sampling error, because the chicks were under observation for comparatively short daily periods, and since the groups were very small samples of this strain of White Leghorns. Other variables to consider may be differences in sex ratios, the relative frequency at which any two birds met, and individual difference in rates of development.

There were some changes in the peck-order of the 9D females and the 9C males after an initial social order was formed. Although such reversals of dominance were expected, these changes raised the question of whether the original peck-order represented the relative levels of aggressiveness of the individuals, or whether any individuals which developed more slowly might have their potential aggressiveness suppressed by low rank attained during the establishment of the order. At the age of 21 weeks the 11 females of 9D were isolated in a laying battery for about six weeks. The procedure permitted further development without stresses associated with the peck-order, and it caused the extinction of dominance relations between penmates (Collias, 1943; Guhl, 1953, present techniques used to measure aggressiveness). The pullets were then matched by pairs in initial encounters until each met each of the others to establish dominance in a neutral area. After one week these birds were paired again for another series of encounters. The pullets were then ranked according to the number of encounters won in each series.

Coefficients of correlation were determined between the number pecked in the original peck-order and the number of encounters won in each series. The results were as follows:

Number pecked: Number of encounters won in first series, $r = +0.77$; $P = 0.01$

Number won in first series: Number won in second series, $r = +0.77$; $P = 0.01$

Number won in second series: Number pecked, $r = +0.61$; $P = 0.05$.

Although these correlations are significant there were changes in the number of individuals pecked as related to the number of encounters won. Four pullets had the same rank in the peck-order and in each of the two series of encounters, the other seven changed ranks from one to six steps between the original order and the second series of encounters, in about nine weeks. The lower coefficient of 0.61 (and barely significant) of this comparison probably indicates that some individuals developed at slower rates than others. Four pullets improved their status and three lost rank. Similar tests with other groups of chicks showed that changes in rank may or may not occur.

Effect of Sex Hormones on Male Chicks

With the background of information obtained from observations on heterosexual groups of chicks, experimentation was begun to determine some of the physiological and psychological factors influencing the development of social behaviour patterns and the establishment of a dominance order. Androgen and œstrogen were known to influence social behaviour in chickens (Allee, Collias & Lutherman, 1939; Allee & Collias, 1940) and other vertebrates (Beach, 1948).

Two sets of experiments were run with male chicks. The first was a test with androgen and the second with œstrogen. Each set used two

groups of chicks; one of which served as a control or untreated group.

In the first set, White Leghorn (Kansas State College strain) chicks were divided at random into two groups of 9 and 10 chicks. The former group was used as a control, and each chick in the latter group received 0.5 mg. androgen daily from the third day after hatching to eight weeks of age. The development of dominance relations are shown in Table IV. There was no difference between the control and the treated cockerels in the span of weeks during which dominance relations were developed, but the injected birds established more peck-rights during the sixth and seventh weeks. The controls established peck-rights at a mean age of 7.75 weeks, the androgen treated males at 7.13 weeks, making a difference of only 0.62 week. It was of interest to note that androgen did not have as marked an effect on domination as it did on other behaviour patterns such as crowing, which appeared a few days after injections were begun (see also Collias, 1950b).

Table IV. The Effect of Androgenic Treatment on the Development of Peck-rights in a Small Group of White Leghorn Male Chicks

Number pecked	Peck-order	Weeks of age 6	7	8	9	10
		Normal ♂♂				
8	GR	1	7			
7	V		2	4	1	
5	Y			4	1	
5	R		2		3	
4	G	1		2	1	
3	RR			2	1	
3	B		1	2		
1	VV			1		
0	VR					
36	Total	2	12	15	7	
		Androgen treated ♂♂, 3rd day—8 wks., 0.5 mg/day				
9	Gh	5	4			
8	Y	2	1	5		
7	RV	1	3	3		
6	RG	2	1	3		
5	RR	1	3	1		
4	V	1	2	1		
3	G		1	1	1	
2	Vh		1	1		
1	RY			1		
0	R					
45	Total	12	16	16	1	

The second experiment was run during the summer and because day-old chicks were not available some four-week old White Rock cockerels were received from a commercial source. In previous experiments no peck-rights developed before the normal male chicks were five weeks old. These chicks were divided at random into two groups, and those in one of these were injected every other day with 1.5 mg of diethyl-estradiol. Right and left sides of the breast were alternated as injection sites. Treatment started on the 28th day and were continued until the chicks were 59 days old.

Table V. The Effects of Œstrogenic Treatment on the Development of Peck-rights in a Small Group of White Rock Males

Number pecked	Peck-order	Weeks of age 5	6	7	8	9
		Normal ♂♂				
9	Rh		7	2		
8	V	1	5	2		
7	Y	1	3	3		
5	R		2	1	2	
5	Yh		3	1	1	
4	Gh		2		2	
4	G		1	1	2	
2	VR		1	1		
1	Vh				1	
0	GR					
45	Total	2	24	11	8	
		Œstrogen treated ♂♂, 28th day-59th day, 1.5 mg/2 days				
9	VR	4	4	1		
7	V		4	3		
6	Y	2	1	3		
5	R	1	3	1		
5	Gh	3	1	1		
5	G		3	1	1	
4	Yh		2	1	1	
3	Vh	1	2			
1	Rh			1		
0	GR					
45	Total	11	20	12	2	

The results are given in Table V. The mean age at which the controls established peck-rights was 6.56 weeks and 6.11 for the œstrogen treated cockerels. The difference is only 0.45 week. Some peck-rights developed during the fifth week of age, or one week earlier than in the tests with White Leghorn cockerels treated with androgen. The peck-order also formed a week earlier, but these differences were not necessarily breed differences (see previous comments on

size of sample and length of observation periods). No differences were noted which may be attributed to experience during the first four weeks, although it might have been a factor. These chicks came from a large group which are called "started chicks" in the poultry industry. The effects of œstrogen appeared to be similar to those of androgen treated chicks only in so far as there was a tendency to develop dominance relations earlier than among the controls of this test. There was a marked difference in behaviour patterns. Before the fifth week it was noted that the treated chicks failed to show any marked aggressiveness; more accurately stated they were rather phlegmatic. Although some pecking occurred, most of the dominance relations were determined on the basis of avoidance. Œstrogen treated chicks at this age were consistent in avoiding certain of their penmates, one of the criteria used to determine dominance status between any two individuals. The social order in this group of experimentals might be called an avoidance-order rather than a peck-order, if the emphasis is placed on negative reactions to specific penmates rather than on the aggressive actions.

Table VI. The Effects of Androgenic Treatment on the Development of Peck-rights in a Small Group of White Leghorn Female Chicks

Number pecked	Peck-order	Weeks of age 6	7	8	9	10
		Normal ♀♀				
8	G	1		2	4	1
8	VR	1	2	5		
7	VV	1	1	4	1	
7	Rh		6	1		
5	V		2	2	1	
4	Gh		1	1	1	1
3	R					3
2	Yh				1	1
1	Y					1
0	Vh					
45	Total	3	12	15	8	7
		Androgen treated ♀♀, 2nd day-8 wks., 0.5 mg/day				
9	VV	2	7			
7	GG	6	1			
6	Y		2	4		
6	G		2	4		
6	Vh		1	3	2	
5	Yh		1	4		
3	Rh		1	2		
2	Gh			1	1	
1	R				1	
0	V					
45	Total	8	15	18	4	

Effects of Sex Hormones on Female Chicks

Two sets of experiments were run with female chicks of a commerical strain of White Leghorns which were received when two days old. Each experiment contained a control group and another of which the individuals were treated with a sex hormone. The chicks were taken at random from the shipping boxes and placed alternately into each of two floor pens.

Each group of the first set contained 10 chicks. The experimentals were injected with 0.5 mg of testosterone propionate daily from two days old through the eighth week. The results are given in Table VI. The treated pullets established more peck-rights during the sixth and seventh weeks than did the controls; they also formed a peck-order about one week earlier. Mean ages for the formation of peck-rights were 8.09 and 7.40 weeks, with a difference of only 0.69 week, which is similar to the results of androgen injection into males.

The second set used for a test with œstrogen presented some problems. The chicks were chilled soon after they were placed on the floor and two died in each group of ten. Aggressive behaviour, when it did develop, was comparatively infrequent and the data were insufficient to ascertain the earliest established peck-rights. This is reflected in Table VII, since no dominance relations were known, with confidence, to be formed during the sixth and seventh weeks. Mean ages were 9.36 and 8.75 weeks for controls and experimentals respectively, with a difference between the means of 0.61 week. The pullets treated with 1.5 mg of diethyl-estradiol every other day did however show a slight advance over their controls. This statement is qualified because autopsy revealed that the alpha bird (VV) was a male, and its early establishment of peck-rights must be disregarded in making comparisons. As with the males receiving œstrogen, consistency in avoiding specific individuals was more frequent than unidirectional pecking. The effects of œstrogenic treatment were an increase in submissive behaviour and a tendency toward an earlier establishment of a social order by means of avoiding reactions.

Development of Peck-Rights in Capons

Commercial hybrid males were divided into four groups at random. The cockerels of three of these groups were caponized. Each group con-

Table VII. The Effects of Œstrogenic Treatment on the Development of Peck-rights in a Small Group of White Leghorn Female Chicks.

Number pecked	Peck-order	Weeks of age 6	7	8	9	10
		Normal ♀♀				
7	V				5	2
6	R				4	2
5	VV				3	2
4	RV				3	1
3	GR				2	1
2	Gh				1	1
1	Vh					1
0	Y					
28	Total				18	10
Œstrogen treated ♀♀, 2nd day-10th w'k, 1.5 mg/2 days						
7	VV*		7			
6	V				6	
5	R		1		4	
4	Y				4	
3	RV				2	1
2	VY				2	
1	RY				1	
0	GR					
28	Total			8	19	1

* Autopsy proved this chick to be a male.

tained 10 chicks at the start, but there was one death among the normal males and another in one group of capons. Chicks were castrated when nine days old by either Professor T. B. Avery of the Department of Poultry Husbandry or by Dr. E. H. Herrick of the Department of Zoology. It seemed advisable to attempt castration of these males prior to the onset of endogenous androgen. Willier (1952) states that gonadotropic activity is present with certainty by the fifth day after hatching, and that from this time on the gonadotropic activity gradually increases. Breneman & Mason (1951) in a critical study of pituitary-gonad relationship began their experiments with chicks 10 days old. It was therefore assumed that caponisation by the 10th day might preclude any conditioning of behaviour patterns by endogenous androgen.

Some comments need to be made here to account for the very high dosages of sex hormones used in this set of chicks. Breneman & Mason (1951) estimated that the physiological level of 40-day old White Leghorn cockerels was under 50 gamma (0.05 mg). Noble & Zitrin (1942) used 0.5 mg of testosterone propionate in cockerels beginning at the age of two days and of 15 days. Collias (1950b) varied the amount injected into two-day old cockerels from 0.1 to 0.7 mg per day and found that the frequency of certain behaviour patterns varied positively with the dosage. Both of these experiments were concerned with the early appearance of certain behaviour patterns. Noble & Zitrin used dead or anesthetised pullet chicks to act as stimuli for the treated cockerels; they also paired cockerels and pullets during experimentation. Collias did not give details of his procedures. He stated that the birds tended to become refractory with continued treatment. A probably similar change was noted by Noble & Zitrin as they found that the copulatory response to a dead or anaesthetised chick was not elicited as frequently after treated males were paired with œstrogen treated females. The question arose as to whether this change to a higher threshold for response was mediated through essentially physiological or psychological factors, and if the latter, could it be bridged by still higher dosages of androgen.

Certain observations have indicated that psychological factors (learned behaviour) may be very important in determining whether a particular behaviour pattern is evoked. It was previously stated that new behaviour patterns appeared and waned in frequency with behavioural readjustment in normal chicks. Peck-orders are evidence of adjustment to aggressive behaviour, and further adjustments have been shown by the relation between sexual activity and position in a social order (Guhl & Warren, 1944; Guhl, 1950). Other instances of the dominance of psychological factors over physiological state were given by Guhl, Collias & Allee (1945); a hen treated with an androgen showed her increased aggressiveness in a discrimination cage long before it became evident in the social interactions of her "home" flock. Similarly, two cocks failed to show mating behaviour in their "home" flock (due to social suppression) but mated readily with hens in another pen. There is further evidence of social inertia in tests with androgen treated hens by the fact that once higher social status was attained it persisted after the exogenous hormone was withdrawn (Allee, Collias & Lutherman, 1939).

The test presented here differed from those referred to above. Attention was focussed on the establishment of peck-rights (social adjustments) and not on the earliest appearance of social behaviour patterns. Therefore the birds were not presented special stimuli but were

disturbed as little as possible even when fed and injected. In an effort to counteract the social inertia caused by adjustments in behaviour, which formed early in the life of the chicks, very high levels of androgen were used.

The results of this set of experiments are given in Table VIII. It will be noted that the normal cockerels began to form peck-rights about as early as the cockerels of other genetic backgrounds, but there was a greater span of weeks before all dominance relations were established and the mean age was 9.92 weeks. Capons treated with testosterone propionate (from the 10th day of age) began to develop peck-rights a week earlier. The mean age of 7.82 weeks was 2.10 weeks earlier. These capons received injections of 0.5 mg per day at the start, and the amount was increased by 0.5 mg. weekly until four weeks old, and kept at that level until nine weeks old. As expected, this treatment suppressed growth (the average body weight was 564 grammes as compared with 905 grammes for the normal males) and injections were stopped although the capons appeared to be in good health. During the next three weeks they continued to establish peck-rights and formed a peck-order about one week earlier than the normal cockerels.

The second group of capons received 2.0 mg daily from the 35th to the 84th day of age. The mean age of peck-right establishment was 8.53 weeks, which was 1.39 weeks earlier than that of the normal males and 0.71 week later than that of the capons injected from the 10th day. The response was immediate as shown by the formation of peck-rights during the sixth week. The delayed injection showed that the immediate response to a suitable hormone must be associated with the level of development. This point is further substantiated by the fact that androgen administrated soon after hatching (in intact males as well as in capons) did not markedly augment the establishment of peck-rights although certain behaviour patterns could be augmented, such as crowing and pecking. Apparently nervous mechanisms associated with individual recognition and ability to form associations between experiences may have not developed sufficiently, or the characteristics serving as the basis for individual recognition were not present (e.g. features of the combs, Guhl & Ortman, 1953).

Turning to the untreated capons of this set, Table VIII, peck-rights began to form a week later than among normal cockerels, but the peck-order was not completed until the 17th week. The mean age was 13.69 weeks and 4.02 weeks later than that of the normal males. Apparently androgen level is not the only factor involved in the establishment of dominance relations. These results indicate that the development of pecking and of peck-rights are basically mechanisms within the nervous system. It is generally known that androgen lowers the threshold for aggressive action (Beach, 1948). The results given here suggest that this hormone has little direct effect on the early development of dominance relations. The greater spread of time during which peck-rights developed in these capons might be related to the low intensity and frequency of pecking among capons (i.e. a high threshold for aggressive behaviour). Scott & Fredericson (1951) found that pain was an important factor in causing non-competitive fighting. The lower frequency of pecking would result in less reinforcement. The ability to make the associations required for the establishment of dominance relations appeared to develop at about the fifth or sixth week of age (see controls in previous tables) under the conditions of these experiments. With stronger or more appropriate stimulation one may assume somewhat different results. This point will be considered later.

There still remains the question of whether these capons were devoid of endogenous androgen. Breneman (1951) considered the probability of the adrenals as a source of androgen in chicks but his experiments gave no such evidence. A number of capons had a portion of a testis remaining, which was noted macroscopically at autopsy. Among the 20 capons injected with androgen, 11 had a portion of a testis (the largest was less than one third of the size of a normal testis). Although a "slip" ranked highest in each of these two groups, these two had the smallest remnant in their group. There appeared to be no relationship between the size of testis material, or lack of it, and social rank. Among the untreated capons, 4 of the 9 retained a remnant and they ranked 2, 6, 7, and 9 in the original peck-order. A "complete" capon was the alpha bird and the "slip" with the largest fragment of testis was in the omega rank. The "incomplete" capons, or "slips", were detected by, or before, the 17th week as the combs were somewhat larger and of a deeper red than those of the other capons.

A test was devised to determine the probable influence of the presence of some testicular tissue on the relative aggressiveness of the individuals in the group of 9 untreated capons.

Table VIII. The Effect of Androgenic Treatment on the Development of Peck-rights in Caponized Chicks as Compared with Normal Cockerels and Capons of the Same Age.

Number pecked	Peck-order	Weeks of age 5	6	7	8	9	10	11	12	13	14	15	16	17
						Normal males								
8	GV				1	3	3	1						
7	GY		1		3	2		1						
6	VY			2	1			1	1	1				
5	V							2	2	1				
3	R						1			2				
3	VV					1		1		1				
3	RY			1	1					1				
1	YY				1									
0	BB													
36	Total		1	3	7	6	4	6	3	6				
						Androgen treated capons, 10th day—63rd day								
9	GB	3	2	1	2			1						
8	GV	5		1	1		1							
7	B		2	1	2		2							
5	R	2		1	1	1								
5	VB		1		2		1		1					
4	Y			1	1	1	1							
4	BB					1		2	1					
2	V						1	1						
1	GR						1							
0	VY													
45	Total	10	5	5	9	3	7	4	2					
						Androgen treated capons, 35th day—84th day.								
9	GV		2	1	3	1	1		1					
7	G		2	1	1	2	1							
6	GB			1	3		1		1					
6	VB		1	2		1	1		1					
5	RR			1	3			1						
5	GY			1	2		2							
3	B					1	1	1						
2	VY				1		1							
1	GR				1									
1	BB						1							
45	Total		5	7	14	5	9	2	3					
						Capons								
8	R									2	1	4	1	
7	GV			1	1		1	2		2				
6	GY				1			1	1	2				1
4	GR							1	1	1				1
4	B								1				1	2
4	VY											1		3
2	GB											1		1
1	GG													1
0	G													
36	Total			1	2	0	1	4	3	7	1	6	2	9

After the 17th week the individuals were isolated in a laying battery for about 4 weeks to extinguish dominance relationships and to allow for further development of gonadal activity. Each bird was then paired with each of the others in a neutral area to establish dominance. The birds were then rated in accord with the number of contests won. This method gave an estimate of the relative aggressiveness of the individuals in this group.

Of the 36 possible dominance relationships in this group of nine capons, the "complete" capons had 23 peck-rights in the original peck-order. The results of the initial encounters gave these capons 17 wins to 19 for the "slips." There were 10 changes in dominance rating; 4 were capons over capons, and 6 were "slips" over capons. This suggested a gain by birds which had some remnants of a testis, as was expected because the birds were now 22 weeks old and testes are usually well developed at this age. However, the changes were not as striking as it appeared at first consideration. The "slip" with the largest remnant was still at the bottom of the rating based on initial encounters. The correlation coefficient between the number of individuals pecked in the original peck-order and the number of contests won was 0.69 (P less than 0.05). Similar tests made with normal cockerels and pullets (Guhl, 1953) also showed shifts in dominance, and the coefficients of correlation varied from less than 0.50 to 0.88. These comparisons do not preclude the possible influence of androgen in the "slips", but raise some doubt as to whether the concentration of endogenous androgen was sufficient to question seriously the results obtained in these sets of capons.

At this point in the investigation an inspection of the Tables II through VIII suggested that individuals ranking high in the peck-order might establish peck-rights earlier than low ranking chicks. Coefficients of correlation between the number of individuals pecked in the original peck-order and the mean age at which peck-rights were established by each individual were calculated for the 16 flocks. All correlations were negative and the coefficients ranged from 0.09 to 0.65, of which 8 of the 16 were statistically significant. This suggests that individuals which mature earliest may assume high rank, which they may retain by reinforcement through pecking activity. If the rates of development are approximately equal between any two chicks, the characteristic level of aggressiveness may determine dominance relations. Several other factors (Allee, Collias & Lutherman, 1939) might influence the outcome of initial pair contests. Birds which develop more slowly, but otherwise are relatively aggressive, may revolt and alter their status as incidences leading to back-pecking arise. Some changes in dominance status were noted after an original peck-order was determined. The results of initial encounters conducted with the White Leghorn pullets in 9D also show shifts in dominance. The relatively low coefficients are indicative of a multifactor situation but definite trends are in evidence.

Effects of Rearing in Partial Isolation

In four of the above sets of experiments some chicks were placed into partial isolation when received, and taken at random as were those composing the afore-mentioned groups. The object of this test was to determine whether the lack of early experience with other chicks influenced the time at which chicks learned to form a peck-order. That is, could chicks reared without the early social experiences associated with the development of frolicking, pecking, fighting, and other social patterns, form a peck-order at the age when the control group became organised.

The isolated chicks were assembled when their respective control group established a peck-order. Six isolated White Leghorn cockerels from the same hatch as those listed in Table IV were assembled when nine weeks old. Observations made during the next 48 hours gave good indications of a peck-order. Although the White Rock cockerels (Table V) were four weeks old when received, 10 individuals were placed into isolation until eight weeks old. These males formed a peck-order within 48 hours. There was no suggestion that the experience of the first four weeks facilitated the formation of a social organisation. Two sets of pullets were also assembled. These were from the hatches listed in Tables VI and VII. There were 7 in the former and 8 in the latter group, and the pullets were 10 weeks old when assembled. The first group was organised after three hours, and the second after eight hours. Short observation periods were made on the male chicks but both pullet groups were observed continuously for four hours after assembly. Males may not establish dominance as readily as females, as suggested here, but the difference may be due,

in part, to the difference in the time spent on post-assembly observations.

The size of the group may be a factor in the time required to form a peck-order. The 6 White Leghorn males had only 15 possible peck-rights, whereas the 10 White Rock males had 45. The pullet groups had 21 and 28 possible dominance relationships. It would be of interest to vary the size of groups formed by chicks reared in isolation to get a measure of the extent to which chicks are able to make associations among individuals. However, individual variations in such development appeared to be great, as may be noted in the span of weeks during which dominance developed in the various groups reared together (Tables II to VIII).

The results of these tests show that chicks reared without the early social experience of frolicking, pecking, and fighting as free bodily contacts, could establish a social order in a comparatively short time. Presumably the stimuli which evoke agonistic behaviour patterns may have been present to some degree in partial isolation, as the chicks could hear and see neighbours. It did not require 5 to 10 weeks of experience, such as inter-individual bodily contacts, to establish peck-rights. Nor can it be concluded from these results that the ability to recognise individuals developed only at these ages. The establishment of peck-rights between any two chicks in group-reared chicks might be augmented or retarded by the persistence of existing behaviour patterns through reinforcement. The question arises as to whether the time of peck-right formation might have as its primary basis the maturation of the nervous and/or endocrine systems. Could chicks reared in partial isolation form a social order when assembled at ages earlier than those at which the group-reared chicks became organised?

Influence of Social Adjustments and Sex Hormones on the Development of Dominance Relations

Two tests were made to determine whether chicks reared in isolation could form a dominance order earlier than chicks reared as a group. This appeared to be probable because the control groups, in previous tests, exhibited adjustments to behaviour patterns existing at a particular age, and new patterns seemed to appear rather abruptly. Chicks reared in partial isolation should not possess such social inertia. The assembly of isolated chicks also introduced a stimulus for aggressive action because the birds would meet as strangers. Both of these tests were with commercial hybrids; one with cockerels and the second with pullets.

The cockerels were divided at random into five groups; a group of 11 untreated controls reared together; a group of 11 androgen treated controls also reared together; and three groups of 10 each reared in isolation which were treated with testosterone propionate (0.5 mg beginning on the 15th day). Androgen was used with the expectation that each individual would have nearly the same concentration of the hormone in its blood stream, and thereby reducing individual variation except for any probable basic differences in thresholds of response to this hormone or of reaction thresholds.

The schedule for assembling the isolated cockerels was somewhat arbitrary. The first group was to be assembled about the time that the similarly injected controls began to show indications of setting up peck-rights, and before the normal controls began to establish any dominance relations. One group was assembled when 31 days old. Ten days later another group of isolated birds assembled, and the third group when 51 days old. Each group of isolates was observed for a week following assembly. The two control groups were observed from the beginning of this experiment until 56 days old, when the test was terminated. In previous experiments many of the males treated with androgen had established some peck-rights at this age.

The results are given in Fig. 2 which shows the total number of peck-rights established in each of the five groups at various ages. The ratios at each curve indicate the number of peck-rights established at that point in relation to the possible number of unidirectional dominance relations in the flock. As expected from previous tests the injected controls established peck-rights earlier than did the normal cockerels, and nearly completed the development of a peck-order at 56 days of age (53 out of a possible 55). The first group of isolates nearly completed a social order (42 out of 45) when 37 days old and exceeded the treated males reared as a group. From this result one may conclude that the inertia associated with inter-individual adjustments in group-reared chicks may have an inhibitory effect on new behaviour patterns even when under the influence of exogenous androgen. On this basis one would anticipate a

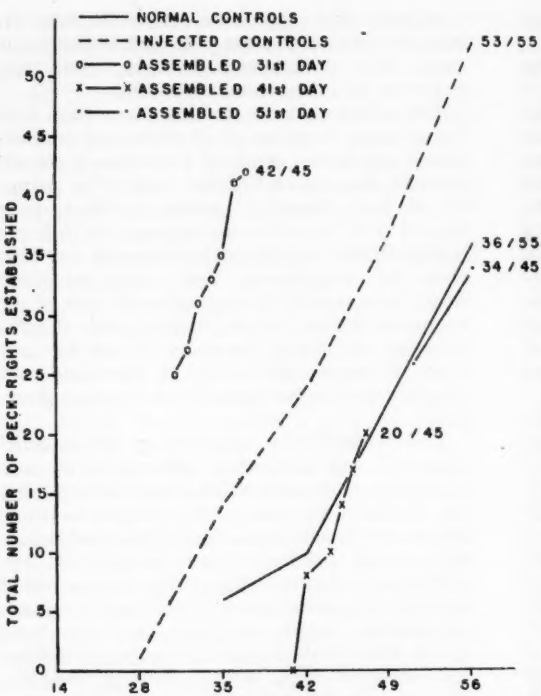

Fig. 2. The total number of peck-rights established at various ages among cockerels reared as a group and others reared in partial isolation and assembled at different ages. The caged isolates and one group, reared together, were injected with an androgen.

more rapid development of a social order in the two groups of similar isolates when assembled at a later age. However the results were strikingly different.

The second group failed to establish any peck-rights during the first day after assembly and formed only 20 out of 45 peck-rights by the end of a week. The third group performed somewhat better. The data (and motion pictures taken during the first hour or longer after assembly) show that these three groups differed in their reactions. The first group began to peck and fight after a few minutes of adjustment to the new situation. Some peck-rights were formed within one hour. Sexual behaviour, such as attempts to mount, occurred early in the week during which they were observed. The initial reactions of the second group, after a brief adjustment period, were almost entirely sexual. Attempts to mount were very frequent. The males responded with a strong negative reaction to such behaviour, and they soon collected at one end of the cage. Under such conditions the aggressive drive appeared to be suppressed for there was no fighting, and no peck-rights were established during the first day. By the second day some fighting developed, and attempts to mount were less frequent. The typical adjustment in this group was to collect in a group and to remain standing (the resting position stimulated mounting behaviour). This was the usual situation for the rest of the week.

The group assembled at 51 days of age started to fight immediately and some peck-rights were established within two hours. Attempts to mount were observed but they were not as frequent as in the second group. By the end of a week only 34 of a possible 45 peck-rights were formed, which was similar to the situation among the normal controls at the same age.

No adequate explanation can be given for the differences between these three experimental groups. The first and third were assembled early in the afternoon whereas the second was assembled early in the evening. It was necessary to choose an hour after which the birds could be observed continually for three or more hours, and there was no known reason for expecting differences due to time of day for birds reared indoors under artificial light. However, a theoretical explanation is possible although it has several questionable aspects.

The level of androgen in the blood stream influences both aggressiveness and sexual behaviour. Although the injected birds received the same amount of androgen daily, the dosage, when related to body weight of growing birds, actually decreased with time. On the 51st day the mean body weights were about twice that at 31 days of age. However, the injected controls continued to establish peck-rights at a fairly uniform rate, whereas the second and third groups approached the rate of the normal controls.

The various behaviour patterns, and/or their thresholds, tend to develop in some order and certainly not all at the same time. This is shown by the fact that high levels of exogenous androgen at an early age did not produce the full repertory of all the adult behaviour patterns. Although aggressive behaviour and sexual behaviour are both mediated by androgen the observations in the experiments reported here

suggest that the former appear earlier than do the latter, with some overlapping (certain components or motor outlets occur in both chains of these two behaviour patterns). Such a sequence is common among feral birds that are seasonal in their breeding. No qualitative study was made which measured intensities of reactions nor were the stimuli evaluated. It may be assumed that at 31 days of age the mechanism(s) for patterns of aggressive behaviour had progressed further in development than those for sexual behaviour, whereas at 41 days the latter had emerged and the birds were assembled before much, if any, extinction had occurred. At 51 days of age and with somewhat lower dosage (per gramme of body weight) a balance between the two drives was being established. Such a conflict between these two drives has been demonstrated by Hinde (1953) in the Chaffinch.

If these interpretations of the results are acceptable at present, then one may conclude that the ability to make associations between individuals (as in peck-orders) in small groups of chicks developed during the fifth week of age. Larger groups would place a strain on this learning process. If more than one behaviour pattern should develop at about the same time (as shown by injections appearing to compress, in time, the sequence in which various patterns matured) then the complexity of adjustments would be compounded; such may have been the situation with the second and third groups when assembled. To this confusion could be added the variability in the development of individuals.

A similar, but simpler, situation was devised with the pullets. In this test there was no complication with sex drive (pullets do not display the receptive crouch until late in development) and no sex hormones were injected. The pullets were divided at random into four groups when received. There were three groups of 10 each which were reared in partial isolation, and 6 controls reared together. The isolated chicks were assembled at 45, 52, and 66 days of age, which was later than with the males since females are less aggressive than cockerels and because there was no androgenic treatment.

In a group composed of 10 individuals there are 45 possible peck-rights. The chicks assembled at 45 days of age established 19 of these during the first day after assembly; and those assembled at 52 and 66 days established 21 of a possible 45 peck-rights each during their first days. The six controls established 12 of a possible 15 peck-rights by the age of 49 days and did not complete a peck-order until 63 days old. Except for the first group of isolates, observations were not continued beyond the first day after assembly. Social inertia among the controls was not obvious under these limited comparisons, in part, because there were fewer individuals (i.e. less social stress) and therefore only one third as many peck-rights as among the experimental chicks. However, by comparison, the isolates assembled on the 45th day showed marked progress as they established 35 out of 45 possible peck-rights by the end of the second day.

The comparisons between the data (Fig. 2) on the group-reared cockerels and the assembled isolates present some other difficulties in explanation. Some sexual behaviour was observed early among the injected controls and somewhat later among the normal controls. The relative infrequency of sexual behaviour among the injected controls, as compared with the treated isolates when assembled, probably was in relation to the gradual adjustments possible in the group and/or to social inertia. Those assembled at 31 days did not display these restraints nor an intense sexual drive at that age. The chicks in this group demonstrated, as did the pullets, that they were capable of making some inter-individual associations, and that at a higher rate than either of the group-reared chicks.

These experiments with cockerels and pullets reared in partial isolation showed that some individuals could establish peck-rights at an early age without the experience of previous bodily contacts. Much individual variation occurred in the development of agonistic behaviour patterns.

Social Inertia and the Display of Agonistic Behaviour

The previous tests showed that chicks reared in groups became adjusted to each other and developed social inertia, and that chicks reared in partial isolation may, after short periods of adjustments, stimulate each other agonistically or sexually when assembled. The problem in such experimentation is to recognise the stimuli which evoke the agonistic behaviour pattern. One cannot, with confidence, state that the chicks did not have the ability to respond just because the behaviour patterns were not observed. It may be that adequate stimulation

was lacking or that social inertia caused suppression or extinction. The tests using chicks reared in isolation and assembled at various ages were designed to provide stimulation, for adults are known to show agonistic behaviour when they meet as strangers. Another attempt was made to induce agonistic behaviour at early ages, using the techniques of shifting flock membership (see Guhl & Allee, 1944).

Forty newly hatched hybrid cockerels were placed at random into four cages of the same floor area. One of these cages was divided into 10 isolation cells, as described earlier. The 10 chicks in the other three cages formed groups. Two types of rotating group membership were started on the third day. A chick from isolation was placed into one of the groups and one from the group was placed into isolation. Shifting followed a schedule of rotation between isolation and this group with replacements made every other day. A similar shifting of individuals was made between the groups in the other two cages. This method required 20 days for a complete round. The experiences of chicks in each of these two plans of rotation differed in that isolated chicks had 20 days during which any adjustments such as individual recognition, if any, or any habits which contribute to social inertia could be extinguished (adults after separation for 21 days meet former penmates as strangers, Guhl & Allee, 1944).

The chicks were observed for only 15 minutes daily per group until eight weeks old, or up to the age at which dominance relations may be established in normal group rearing. The data included sparring, pecking, fighting, and avoiding reactions. The results are given in Fig. 3 for each of the three groups with shifting membership. The group of cockerels shifted from isolation showed a markedly higher frequency of agonistic behaviour than did those of the groups in which there was an intergroup transfer. This difference appeared to be due to the greater stimulus provided by the chick taken from isolation and to social inertia in the other two groups. Although there was much variation among individual chicks in both sets of tests, those admitted from isolation were most involved in interactions. The isolate often appeared very alert, with tail and head held erect or, if a relatively unaggressive individual, it showed marked escape tendencies which stimulated pursuit. Some were inactive in these respects and evoked little reaction when placed into the group. The chicks entering a group from a group typically did not display the stance associated with alertness or strangeness. They often preened, fed, joined or avoided the others in the cage. It appeared that habits of behaviour were carried over from group to group as a form of social inertia. A chick shifted from isolation into a group probably lost such habits after 20 days of separation, and in addition it entered a spacious cage. These factors may have augmented any strangeness which it may have sensed.

In addition to the more frequent display of these behaviour patterns the chicks taken from isolation also showed these patterns of behaviour earlier than did the intergroup shifting in-

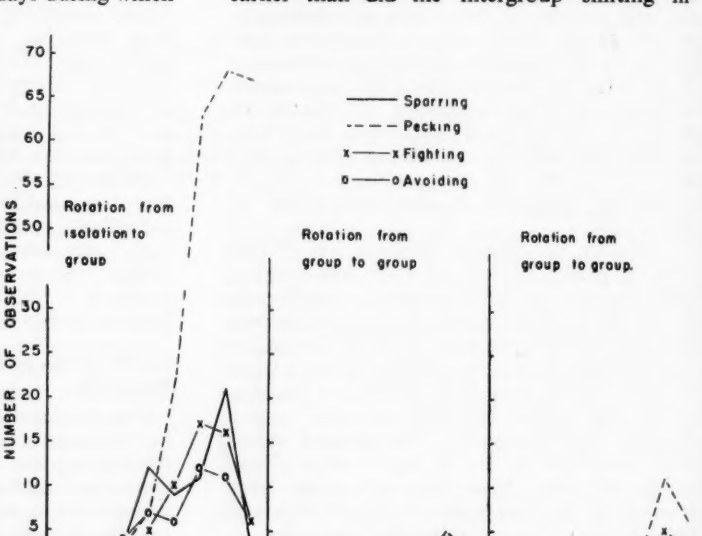

Fig. 3. Differences in the frequency of some behaviour patterns of cockerels rotated between isolation and a group, and those rotated from group to group. The latter show social inertia.

dividuals. The order of emergence varied somewhat from that mentioned previously, but least so in the group shifted from isolation. Under such changing situations one might expect the avoiding or escape reactions to be evoked more readily, and except for avoidance, the order in this group was essentially as anticipated from previous observations. There is also a suggestion that under high stimulation psychologically, as under highly altered physiological conditions with injected androgen, that the ages at which these behaviour patterns appeared initially were not only earlier but spread less in time.

This test demonstrated social inertia in group-reared chicks, and also showed that agonistic behaviour patterns may appear earlier under certain experimental situations than under what might be considered a more normal developmental situation for these domestic birds.

Discussion

In developmental studies of behaviour one is impressed by variability and adaptability. Variations occur not only among individuals but also in time, and the individuals must adjust to both in order to maintain themselves and the group. The history of development is one of change and adequate adaptation.

Individual variation in agonistic behaviour is evident in the peck-order of adults as a gradient in levels of aggressiveness and/or submissiveness. Intragroup variations reported here in the development of behaviour patterns were anticipated, although some may be due to sampling errors. It is not to be assumed that they suggest the limits of variability for the strains or breeds used. Changes in individuals showed differences when viewed as rates of development, whether in behaviour patterns as given here or in body weights or comb sizes which have not been included in this report.

Each individual must adapt itself to developmental changes within itself, particularly such as influence its behaviour, but also to alterations in the behaviour and appearance (as familiar objects) of its penmates. The growth of feathers, comb and wattles result in marked modification of contour, colour, and facial patterns, which would require constant learning if individual recognition were critical at these developmental stages. It might be assumed that social adjustments are simplified during the early weeks by the importance of vocalisations in hen-chicks and chick-chick relationships (Bruckner, 1933; Collias, 1952; Collias & Joos, 1953).

There is relatively little information on physiological developments during the post-hatch life of the chicks, especially such as may influence behaviour patterns. Willier (1952) has reviewed some interesting pituitary-gonadal relationships and summarised them in a chart giving changes occurring over certain spans of time during incubation and post-hatch. Breneman & Mason (1951) have shown that there is a marked increase in the secretion of androgen in the male chick at about 30 days post-hatch. This is about the age at which cockerels began to establish peck-rights (e.g. normal males, Fig. 2).

Other physiological developments which may be worthy of note were summarised by Sturkie (1954). Erythrocyte number and hematocrit increased in relation to androgen. Hemoglobin values increased and thrombocyte number decreased during the same time. Body temperature of day-old chicks is about 3°F below that of the adult but at 10 days is about the same as the adult. Temperature control develops from seven days to three weeks of age, around the time of juvenile plumage. The greatest increase in the secretion rate of thyroxine in White Leghorn cockerels is during 4-12 weeks, which is the period of greatest growth and also the time of peck-right establishment. Adrenal size, in proportion to body weight, decreases during early weeks of life. These items are of interest as they reflect, in part, a stress syndrome during early days or weeks. Garren & Shaffner (1956) found that periods of exposure to cold caused an adrenal hypertrophy. Adjustments to the inadequacy of temperature control are also reflected in early social behaviour. Recently hatched chicks do not approach one another until after experiencing some minutes of bodily contact (Collias, 1950a). Warmth from other chicks (or a hen), as well as vocalisations (Collias, 1950b) form the primary family bonds and facilitate aggregation and socialisation. Centripetal social forces are established long before centrifugal forces caused by the development of agonistic behaviour, which is the subject of this report. Apparently these early adaptations have a permanency similar to imprinting (Lorenz, 1935).

There was some indication that certain behaviour patterns tended to appear in a sequence but with much overlapping. These observations were not under critical study and

the order of emergence cannot be given as definite for several reasons. Although the chicks of each set were from the same hatch, they were not necessarily of the same age in terms of hours. In large hatches the chicks are not removed as they hatch, and some may be as much as 24 hours older than others. Behaviour patterns, such as pecking, fighting, and sexual behaviour, which appear later than others, at least in frequency and intensity, may be influenced less by hourly differences in age. Some experiments, such as those of Noble & Zitrin (1942), Collias (1950b), and certain sets of this experiment have shown that exogenous gonadal hormones may cause some precocious development of certain of these behaviour patterns, particularly agonistic and sexual behaviour. Differences in the results as recorded according to the earliest appearance may be due to a number of factors, such as size of sample, dosage of hormone, and the stimulus situation.

Wood-Gush (1957) reported indications of such a sequence in chickens but was chiefly concerned about the order in which aggressiveness and sexual behaviour emerged. He postulated that aggressiveness may respond to a lower level of testicular hormone than does sexual behaviour, or that either drive might depend on the interaction of this hormone with one or more other specific substance(s). As shown by the results given in Fig. 3, more attention might be given to stimuli which evoke these behaviour patterns. One might also assume that differences in sensitivity to certain stimuli (possible releasers) may occur at various ages, as Beach (1955) has suggested. That is, development is dependent upon various inherent characteristics, including its sensitivity to external influences. This capacity for response is not constant or stable, but tends to rise and then decrease so that critical extrinsic factors can exert their normal effects only if present when responsivity is high. Certainly there is a similarity between certain behaviour pattern sequences in ontogeny and similar ones in the development of reproductive behaviour in cyclical feral birds (e.g., Collias & Taber, 1951; Petersen, 1955). The study of this aspect of behaviour in chicks could be facilitated if there were better information on the specific stimuli which evoke specific patterns of behaviour, and if one could standardise these stimuli as attempted by Fisher & Hale (1957) for adult cocks.

For some years the writer has questioned what Kortlandt (1955) has called the "preformationist doctrine" of instinct, and was attracted by his statement that "hierarchy of instincts serves to shape non-instinctive behaviour patterns during ontogenetical development." That is, that there is no dichotomy of innate behaviour and experience any more than that anatomy and physiology can be considered independently in any final analysis. About 15 years ago we acquired a cock which had been reared by children who obtained it as an Easter gift. This bird had never seen a chicken after it was separated from other chicks of its hatch. When fully mature, in the following fall, it was placed with adult hens which it avoided immediately and flew to the roost. Sexual approaches were made toward the observer. After some days it tried to mount a hen, and in its first attempt it mounted backwards; instead of treading it stood on the crouching hen and crowed. Although the behaviour patterns improved in orientation, it did not become very efficient during the several weeks it was observed. As a result of this observation the isolated chicks of the present experiment were permitted to see and hear each other, to come into close proximity of each other, and limited only in their ability to peck each other, thereby reducing any abnormal behaviour to a minimum. Aberrant behaviour was reported by Fisher & Hale (1957) in cockerels reared in visual and spacial isolation.

Leherman's (1953) clear statements are worthy of inclusion here. "It has become customary, in recent discussions of the 'heredity-environment' problem to state that the 'hereditary' and 'environment' contributions are both essential to the development of the organism; that the organism could not develop in the absence of either; and that the dichotomy is more or less artificial." . . . "The problem of development is the problem of the development of new structures and patterns, within the organism and its internal environment, and between the organism and its outer environment. At any stage of development, the new features emerge from the interactions within the current state and between the current stage and the environment. The interaction out of which the organism develops is not one, as is so often said, between heredity and environment. It is between organism and environment ! And the organism is different at each different stage in its development."

Although the emergence and interrelation-

ships of behaviour patterns need more critical study than that made during the observations given here, some further discussion might be of value. Frolicking is a rather simple spontaneous behaviour which appeared quite early and most often during the stimulation caused by disturbances such as filling feed troughs and turning on the room lights. When two frolicking chicks ran together, they would jump up and down making head thrusts toward each other. This was called sparring and no pecks were delivered. The stimulus for sparring seemed to be a contact with another chick when both showed excitability during frolicking. Pecking occurred quite early and infrequently, but later became associated with sparring and thereby became fighting, which often ended without a decision during the early stages. Pecking and avoidance during the early weeks was bi-directional and later became unidirectional, and peck-rights were established, indicating that an association of aggressive behaviour with a particular individual appeared later. The point of interest is a suggestion of what Kortlandt (1955) called the pathfinding function of instincts in which the innate patterns act as organisers during development of non-instinctive behaviour. That is, owing to ascending maturation and integration "the characteristics of the objects toward which the bottom-level instincts have become conditioned are subsequently taken over by the next-higher-level instincts and largely constitute the characteristics of the objects toward which these instincts appear directed as soon as they mature." However, it is not clear just how this integration occurs. The mechanisms by which innate and acquired behaviours are integrated appear to be hypothetical but the importance of the interplay between extrinsic and intrinsic factors is recognised (Beach, 1955).

Evidences of learning in chicks have been summarised by Wood-Gush (1955) and Thorpe (1956). Whether or not the integration of behaviour patterns mentioned above are accomplished by some type of learning or by some neurophysiological changes implied by Kortlandt's concept of priming, or both, cannot be determined by the data presented here. The injection of exogenous gonadal hormones is followed by precocious behaviour, but such treatment does not produce the full repertory of adult behaviour patterns with the same number of daily injections, Crowing occurs early whereas pecking is less frequent, and both increase in frequency with high dosages of androgen (Collias, 1950b); and mating behaviour appears to have a higher threshold but may occur if adequate stimulation is provided (Noble & Zitrin, 1942). Learning is most evident during and following the establishment of the peck-order.

Some aspects of learning are evident during the formation of a peck-order among adult chickens of either sex. When unacquainted birds are placed together they soon engage in pair-contests, the outcome of which settles dominance-subordination or peck-right relationships. These encounters may vary considerably in intensity, from passive submission by one of the contestants to strenuous fighting which at times is repeated. The stimuli which may evoke either aggressive or submissive acts are yet to be analysed. Fisher & Hale (1957) have made some progress in this direction; Foreman & Allee (1954) have noted that postural stance influences the outcome of such initial contests. The lack of individual recognition (Guhl & Ortman, 1953) appears to evoke non-competitive aggressive behaviour whereas posturing may determine the type and intensity of agonistic behaviour which ensues.

The winner of these contests thereafter asserts its dominance by repeated pecking or threatening while the loser submits or avoids the dominant, thus reinforcing the decision reached at the first meeting. Hard fought encounters may be followed by more intense reinforcement activity. Habits of either attack or escape are formed between all pair combinations in the flock, and these constitute the peck-order. As the recognition of individuals improves and appropriate reactions are facilitated, reinforcement wanes to the point of extinction in very small flocks, or to the level of symbolic threatening. The result is the social inertia which well acquainted flocks show as toleration (Guhl & Allee, 1944). Deviations from such behaviour, as back-pecks, are rare and, if they do occur, are followed by the reactivation (reinforcement) of delivered pecks or, failing that, in a reversal of dominance.

Returning to the behaviour of chicks which were shifted regularly between groups and from isolation into a group (Fig. 3), it was noted that the level of agonistic activity was lower among group-reared chicks. This difference may be attributed to some type of learning or adaptation to group living (i.e. social inertia) which was carried from group to group, whereas chicks

in isolation lost appropriate adjustments. It was mentioned that chicks entering a group from isolation reacted to the new situation and that their stance stimulated residents to react. Apparently the ability to recognise individuals was not developed during much of this test since chicks transferred from group to group did not show the typical reaction that adults do under similar situations (Guhl & Allee, 1944). Differences between these groups of changing membership began to appear prior to the age at which chicks typically began to form peck-rights, indicating individual recognition. One might also consider the possibility that chicks coming from isolation had not learned (or extinction had occurred) that to assume a certain stance might provoke an attack. The indications are that some type of social adjustment or learning may occur prior to the age at which peck-rights are developed. Smith (1957) found that chicks at 10 days could discriminate partners of the same breed but from a different flock.

The kind of social organisation found in a species is determined by the behaviour patterns characteristic of the species. All breeds and/or strains of chickens which have been studied (Potter, 1949; Holabird, 1955; Banks, 1956) have shown very similar organisation, but differences between breeds have been suggested in the intensities of agonistic behaviour (Allee, Foreman & Banks, 1955; Hale, 1954). Studies are now underway at our experiment station, and at others, on mixed flocks. Information on the comparative development of behaviour is needed to determine the relative compatability of several breeds or strains in such mixed flocks, and to learn whether early experience might influence adult behaviour or the ranks of breeds in the peck-order. Experiments on the inheritance of aggressiveness have been conducted during the same years as the observations on the development of social behaviour in chicks; and the results will be published elsewhere.

Summary

1. Certain behaviour patterns tended to appear in a sequence as escape reactions, frolicking, sparring, aggressive pecking, avoiding re-actions, and fighting.

2. In heterosexual groups of chicks pecking occurred between the sexes with males pecking more often on all chicks and more frequently on the males. The limitation of agonistic behaviour between members of the same sex developed gradually.

3. Males established dominance-subordination relationships, peck-rights, and a peck-order earlier than females.

4. Both males and female chicks treated with gonadal hormones formed peck-rights and a peck-order somewhat earlier than did untreated chicks of the same hatch. Androgenic treatment caused an increase in aggressiveness, whereas œstrogen treated chicks were more submissive than their controls and showed more instances of submission than domination.

5. Capons showed much variability as to the age at which peck-rights were established, many were formed long after their normal controls developed a peck-order. Androgenic treatment of capons reduced the age at which dominance relations were established.

6. Chicks of either sex reared in partial isolation (non-contactual) established a dominance order in a matter of hours when assembled at the age at which group-reared controls formed a peck-order. These results suggest that the age at which peck-rights form is determined essentially by processes of maturation rather than of learning only. The indications are that the development of nervous mechanisms were involved.

7. Androgen treated cockerels reared in partial isolation were assembled at various ages during which group-reared controls were establishing their peck-rights. Isolated cockerels assembled at 31 days of age nearly established a social order within 6 days and much earlier than the controls. Two groups assembled at 41 and 51 days failed to show much advance over group-reared normal cockerels. The indications were that at these ages there was a conflict between aggressive behaviour and newly developed sexual drive which required more time for social adjustments. The sex drive in pullets appears much later than in cockerels and a similar test with normal pullets (untreated) did not show this conflict resulting from an overlapping in the development of aggressive and sexual behaviour patterns.

8. Social inertia was demonstrated by shifting chicks regularly between partial isolation and a group, and also shifting chicks between two groups. Chicks shifted from group to group carried with them certain behaviour patterns

whereas chicks from isolation evoked agonistic behaviour.

Acknowledgments

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AN AUTOMATIC FEEDING BATTERY FOR SMALL ANIMALS

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Behavioural work on rodents, and other small animals, frequently demands maintaining the animals on a rigorous feeding-fasting schedule, for many weeks or even months. In order to reduce the labour entailed in this work, we have developed and constructed a set of automatic feeding cages which make food available for set periods daily at preselected times. This mechanisation of the feeding routine has released the experimenters and laboratory staff for other duties and has been entirely successful in its operation. The method described in this paper has been applied for several years. During this period a number of cages and associated feeding mechanisms have been in use. It has been our practice to have animals constantly available for experimental purposes and rats were kept on a 22-hour hunger regime. Although bodyweight losses were marked during the first ten days, there was little loss thereafter for as long as three months.

General Description

Automatic feeding is a method of giving animals access to food between previously determined times (e.g. 6 p.m.-8 p.m., 3 a.m.-4 a.m., etc.)—and only those times—without the intervention of laboratory staff. This was achieved by constructing a battery of home-cages in which each cage had a sliding door or similar device that separated the animal from the food hopper containing small pellets. This door was maintained in the closed or open position during fasting and feeding times respectively. It was operated by an electric motor which was governed by a specially constructed clock and associated switchgear.

A general view of the complete battery (9 cages accommodating approximately 46 rats) is shown in Fig. 1. At one end, the clock and switchgear were mounted laterally. Since the circuits of the cages were independent of each other, it was possible to arrange feeding times for different cages at different times of the day. This was the practice usually adopted in our laboratory and ensured that animals were always available for experimental sessions.

The Individual Units

(i) *Type* 1 *Cage*. The original cage was of the type in which the food trough itself was propelled in and out of the cage. One end of the cage was replaced by a Duralumin plate, having a rectangular hole (approx. 10 inches wide by 2 inches high) to allow the food trough to protrude. When the trough was withdrawn it closed up the hole, except for a small clearance left to prevent animals getting their paws caught. A government-surplus dynamotor having a reduction gearbox was converted to a mains voltage motor and used to drive a worm. The drive was transmitted by the worm to teeth attached to the underside of the food trough. Two interlocked post-office relays operating on the 24-volt D.C. control circuits selected the direction of movement and two micro-switches limited the travel of the food trough. A manual resettable drop-arm indicator was fitted, to show that the food trough had been "in" and "out" of the cage.

(ii) *Type* 2 *Cage*. The second cage, which has been adopted as the standard type, also had one end replaced by a Duralumin plate. This plate had an aperture 2 inches square behind which was a door that opened by sliding upwards thus giving the animal access to a fixed food trough. The motor used was an ex-government 24-volt unit with an incorporated reduction gearbox, and this was arranged by means of a worm drive to move a saddle along a vertical lead screw. The door was hung from this saddle by a chain. This method was employed to avoid possible decapitation of animals, but later models of the cage (see Fig. 2) whilst retaining the same degree of safety were simplified by dispensing with the chain. The saddle also engaged the micro-switches used for limiting the travel. The motor switching was similar to that described above.

(iii) *Clock Unit*. The Clock Unit is basically a digital counter. A government-surplus electric clock movement (one revolution of the hand per hour) was fitted with a cam and micro-switch to "make" for about two minutes at every hour. This micro-switch operated a Post Office-

PLATE IV

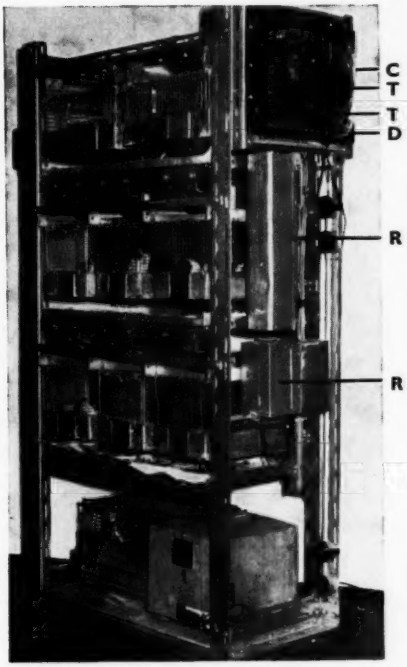
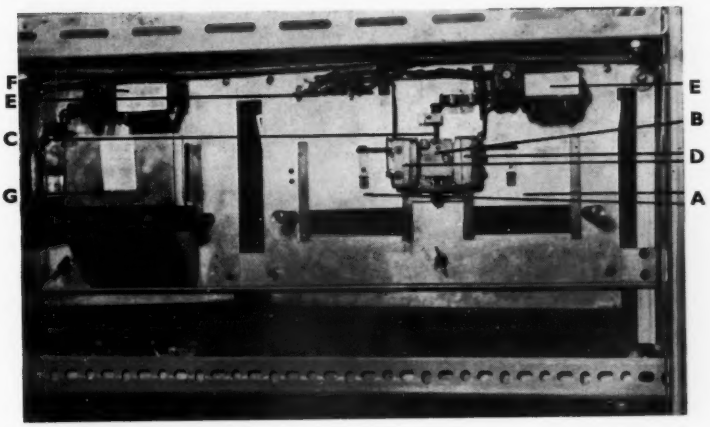


Fig. 1 (*left*). The Complete Battery. The rear view of the top two cages (Nos. 7 and 8) are shown in Fig. 2. The bottom cage is the "type 1 cage". The figure shows also the clock unit C and the distribution panel D with their two respective tag boards T, and the relays R.

Fig. 2. (*below*) Rear View of Cages 7 and 8. The twin food hoppers of cage 7 have been removed to show the sliding doors A, the saddle B, the lead screw C, the micro-switches D, the motor E, and the tag board for electrical connection F. A part of cage panel 8 is visible with food hoppers G in position.



type uniselector, which was arranged to count the 24 hours in the day. The contacts of one uniselector arc were wired to a tag-board, and the wiper of this arc was arranged to be +24 volt in respect of a common return terminal for the duration that the micro-switch was on the "make." Thus, for about two minutes at every hour, the Clock Unit provides 24-volt D.C. at the tag corresponding to the appropriate hour (there are 24 tags for the 24 hours) for opening and closing the cage doors. The Unit was also fitted with a no-volt relay, to operate an alarm bell in case of power failure.

(iv) *Distribution Panel.* A tag-board on a distribution panel was used as power input to the individual cage circuits. Besides a common negative terminal, two tags were used for each cage: one to "open" or make food available, and the other to "close" or take the food away.

Tags on the clock-unit were joined by soldered links to tags on the distribution-panel. This arrangement allowed flexibility of operation. Any one or any number of cages could be "opened" or "closed" at the completion of any hour in the twenty-four; if desired, the same cage could be "opened" and "closed" several times a day. (There would be no difficulty in constructing a clock-unit to operate in, for instance, half-hourly units).

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PROCEEDINGS OF THE ASSOCIATION FOR THE STUDY OF ANIMAL BEHAVIOUR

An Ordinary Meeting of the Association was held on 21st and 22nd March, 1957, in the Department of Zoology, Oxford. The President, Dr. Tinbergen, was in the Chair, and the following papers were read.

AN ANALYSIS OF THE STIMULUS SITUATION RELEASING FOOD-BEGGING IN THE BLACK-HEADED GULL

By R. WEIDMANN and U. WEIDMANN*

Department of Zoology, Oxford

A young Black-headed gull (*Larus ridibundus*) begins pecking at the bill of its parents a few hours after hatching. This may lead to the parent regurgitating food. What makes a chick, which has neither been fed, nor seen another chick being fed, behave in this way? A full answer to this question should include:

(1) a list of the stimuli releasing the begging (pecking) response in an inexperienced chick,

(2) an account of the physiological mechanism responsible for this behaviour,

(3) suggestions on the evolutionary history of releasers and releasing mechanisms involved.

Chicks which hatched under cardboard boxes in an incubator were presented with various cardboard models or rods in succession and the number of pecks they gave to each model within 30 sec. was recorded. The results were subjected to statistical analysis.

The main conclusions can be summarised as follows.

(*a*) In order to release pecking at all, a relatively small object had to be held near and in front of the chick's bill.

(*b*) Movement, position, width, colour and brightness of the model were shown to influence the response; thus more pecks were released by a model whose lower end was at or below eye level than by one held higher; more by one (rod or circle) moved to and fro than by one held still or moved up and down; more by a narrow than by a wide rod; more by a rod held vertical than by one held horizontal; more by red models, and one particular blue model, than by models of other colours, etc. The colour, shape, presence or absence of more distant parts of the model, i.e. its "head" and "neck" region, did not affect the pecking, provided that the red "bill" region was held near the chick.

The effective stimuli fit the natural situation very well, and as far as the analysis goes, they are identical with those found by Tinbergen & Perdeck (1950. *Behaviour*, **3**, 1-39) for the Herring gull (*Larus argentatus*). No definite conclusions about the evolutions of this intimate relationship between the natural stimulus situation and the releasing mechanism (IRM) can be made until more species are studied.

It is suggested that the IRM may involve the whole physiological system between stimulus and response, i.e. the selectivity of a response may not be due exclusively, if at all, to the filtering of information by the central nervous system. Thus the selectivity of the begging response might partly be due to the limitations of the visual field, peripheral adaptation and distortion, simultaneous contrast, filtering of light by yellow oildroplets in the retina and other physiological properties of the eye. The conclusions reached are still highly hypothetical but they have led to a renewed and more penetrating enquiry about the nature of the relevant stimuli.

The responsiveness of the chicks increases with increasing age. It falls when they are fed and only gradually recovers. Heterogeneous summation of various stimuli was studied and it was found that differences occur in the nature of the process: thus the separate effects of two stimuli would "summate" arithmetically (i.e. show no interaction) when presented in combination in some cases, but not in others.

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THE AGES AND OCCUPATIONS OF HONEYBEES ATTENDING THEIR QUEEN

By M. DELIA ALLAN

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The queen of a honeybee colony is usually surrounded by a circle of workers, some examining her with their antennae, some licking her, and an occasional one supplying her with food. Observations on two colonies showed that the number of attendants was greatest when she was stationary, lower during the act of egg-laying, and reaching a minimum when she was moving actively over the comb. This progressive decrease is not unexpected, since the greater the activity of the queen the more likely she is to lose contact with her attendants. Detailed counts demonstrated clearly that at any one time many more attendants were engaged in examining than in licking, even though the exact proportions of the two groups fluctuated according to the queen's activity. This fluctuation is best illustrated by the ratios of "lickers" to "examiners" in the two colonies studied during the summer, being 1 to 8 when the queen was stationary, 1 to 23 when she was laying, and 1 to 88 when she was moving.

Results of observations made to ascertain the ages of the attendant bees showed that while examiners and lickers (147 records) ranged from a few hours up to 36 days old, those supplying food (65 records) had the limited age range of 1 to 11 days, thus supporting the hypothesis that only nurse bees feed the queen. A comparison of the ages of these "feeders" before and after the onset of queen cell formation showed that bees up to 11 days old were found in the earlier period, but that none older than 6 days was observed during the period of swarm preparations.

THE PERCEPTUAL WORLD OF ANTS

By D. M. VOWLES

Department of Psychology, University of Reading

Previous studies of the stimuli used by ants to orientate while homing have been analytical in nature, and have aimed at identifying which stimuli are used, either by limiting the stimuli available to one, or in a complex situation by changing one stimulus at a time until gross disorientation resulted. The work reported here was an attempt to provide the ant with two or more controlled stimuli and to investigate the effect on the accuracy of orientation of varying these. Three types of experiments were done.

1. Ants were trained to retrieve their pupae from the centre of a circular arena. The accuracy of their orientation was measured by recording the lengths of their tracks. When a steady minimum had been reached the stimulus situation was changed, while an ant was at the centre of the area, and the resulting track recorded. Three stimulus conditions were used—a white arena roofed with polaroid, a white arena with a black stripe at one side, a white arena with a black stripe and roofed with polaroid. It was found that the shortest tracks under control conditions were obtained when polaroid and stripe were present, the next shortest when only the stripe was present, and the longest when only polaroid. This shows that with two stimuli present the accuracy of orientation is greater. If both stimuli were removed the ants were disorientated completely. If ants had learned with both stimuli present then changing one stimulus did not disorientate them, but decreased the accuracy of the homing to a level comparable with that found when only the unchanged stimulus was present.

2. Ants were trained to retrieve their pupae from the centre of a large arena. The arena was illuminated from a light, which could be plane polarised, and which could be placed in any position in the hemisphere of "sky" above the area, by moving its supporting trolley. Under these conditions ants utilised stimuli from the trolley itself, the direction of the light and the plane of polarisation of the light. The accuracy of orientation was measured in terms

of the width of the narrowest band on the floor of the arena which would just include all of a single track. In normal, undisturbed ants this band width was greater for the outward than the return track of an ant. In experiments when any one or more of the stimuli listed above were changed after an ant had completed its outward track, the ant was seldom "disorientated," but its return track fell within a wider band than its outward track. Thus where a variety of stimuli were available changing a single stimulus did not disorientate the ant, but caused less accurate homing. These experiments were performed in collaboration with J. Court.

3. Ants were trained to run a T-maze in order to escape from peppermint odour and to return to the nest. The stimuli available were colour maze linings, plane of polarisation of light in the two alleys, direction of light, visual landmarks near the maze, and the leftness or rightness of turn. Changing any one or two of these stimuli after the ant had learned caused the brief occurrence of a few errors which were rapidly eliminated. The sequence in which the changes were made seemed unimportant. If only one stimulus was held constant and the others varied on successive trials no ant learned within 30 trials, although in controls the average learning period is 14 trials. Ants which had been trained in a visually cued maze with one eye covered had to relearn the maze after removal of the eye cover, and gave no evidence of inter-ocular transfer.

It was suggested that the above results might be interpreted as meaning that ants learn to orientate to the visual field as a *whole* and do not necessarily have a perceptual world like our own in which figures are distinguished from their ground and different objects from each other.

SPECIFICITY IN RESPONSIVENESS IN RELATION TO IMPRINTING AND "CURIOSITY"

By R. A. HINDE

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1. No animal can respond to all the stimuli impinging on its sense organs: selection must occur. The problem of the nature of this selectivity is particularly acute in those species-characteristic behaviour patterns for which certain parts of the total stimulus situation (sometimes called sign stimuli or releasers) are more important than the rest.

2. Selective responsiveness to sign stimuli has been explained by postulating a "releasing mechanism" in the animal which can be "unlocked" only by a particular "key." This analogy stimulated much research into the nature of releasing stimulus situations, but has led to an exaggeration of the specificity of the stimuli needed to elicit many behaviour patterns. Thus Tinbergen's studies of the stimuli eliciting gaping or pecking in young birds show not only which stimuli are most effective, but also that the responses can be elicited by a wide range of stimuli. Studies of imprinting demonstrate the initially generalised nature of the stimuli for following in nidifugous birds.

3. Variations in specificity can often be understood in functional terms. Thus responses to predators are usually elicited by a wide range of stimuli, for it is better to be safe than sorry. On the other hand, in mating behaviour, where natural selection may act against hybridisation, specificity is achieved by one or a succession of responses which can be elicited only by a limited set of stimuli. In nest-site selection, which demands both the ability to use the best site available and also the ability to make do where necessary with a poor one, a different type of selection operates. In general specificity in responsiveness will be selected for only if responses to inappropriate objects occur to a disadvantageous extent: further specificity might cause elimination of appropriate responses. The importance of selection for specificity will thus be diminished where inappropriate responses are unlikely or of little consequence: further, its effectiveness may of course be limited by the effectiveness of the sensory and perceptual apparatus.

4. The social responses of many adult birds depend on a responsiveness to another individual in a particular posture, coupled with a sense of size and pattern constancy. The parents of nidifugous species may appear in many shapes, sizes and colours, according to conditions. Until

the young develop a sense of size and pattern constancy, responsiveness confined to a limited range of shapes and sizes would be too specific, for appropriate responses might be eliminated.

5. Selectivity in response to stimuli may be due to the properties of the sense organs (e.g. Lehrman, Schneirla, in Macy Foundation Report on Group Processes, 1956) or the central nervous system. Learning (both habituation and positive conditioning) is important in the increase in specificity during ontogeny. The processes involved are at least superficially similar in parent-offspring relationship, nest-site selection, etc. (see William James' law of inhibition of instincts by habits). Variation in the rigidity of such learning can again be understood in functional terms (e.g. long lasting in parent-offspring relation, short term in feeding).

6. Curiosity and exploratory behaviour are elicited by an extremely wide range of stimuli, which becomes narrowed by habituation. Curiosity is shown especially to stimulus situations which resemble those eliciting specific responses, and thus may play a part in limiting the range of stimuli effective for them (cf. Thorpe, 1956, *Learning and instinct in animals*). It is also shown to normally adequate stimulus situation when motivation is low.

SOCIAL BEHAVIOUR IN FOUR BANK VOLE RACES

By JOHN GODFREY

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Bank voles from the mainland of Great Britain and those from the islands of Raasay, Mull and Skomer are morphologically distinct but will interbreed if given no choice of mate, yielding fertile hybrids. Differences in behaviour associated with the variations used by taxonomists, and also whether these differences result in reproductive isolation in mixed experimental communities, have been investigated.

The frequencies with which a vole occupied its favourite nest box, and defended it against intruders, were used as criteria for territoriality. Skomer voles were found to be markedly less territorial than the others. Cues from inside the cages, and from the nest itself, were less important than those from outside the cage in the recognition by a vole of its home site.

In small communities of voles from the same population there was a tendency for the members, especially if female, to be found in groups more frequently than would be expected by chance. This is considered to demonstrate gregariousness. Social groups consisting of a male and a female from the mainland and another pair from one of the island populations were less gregarious. The constitution of associations showed racial segregation. Males from Raasay and Mull, but not from Skomer, were usually found in associations excluding the mainland male. Olfactory cues were sufficient for this racial discrimination.

As well as being less aggressive, Skomer animals did not show either of the submission signals found in other voles. Hybrid offspring of Skomer mothers tended to die at weaning age as a result of fighting among themselves. The reciprocal cross led to less fighting and no deaths. It is suggested that the development of submissive responses depends on specific behaviour by the mother.

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ETHOLOGICAL CONVERGENCES IN SATURNIIDS

By A. D. BLEST

Department of Zoology, University College, London

For précis see Proceedings of 24th October, 1957.

FURTHER WORK ON COLOUR-CHANGE MECHANISMS AND BACKGROUND SELECTION IN XENOPUS

By R. WHEELER
Oxford

OLFACTORY THRESHOLDS FOR FATTY ACIDS IN DOGS

By D. G. MOULTON
Department of Anatomy, University of Birmingham

EXPLORATION AND AVOIDANCE IN WILD AND LABORATORY RATS

By S. A. BARNETT
Department of Zoology, University of Glasgow

THE BEHAVIOUR OF EXPERIMENTAL VOLE POPULATIONS

By D. CHITTY
Bureau of Animal Population, Oxford

No précis of these papers were available at the time of going to press

An Extraordinary Meeting of the Association was held on 8th May, 1957, at University College, London. The following paper was read.

THE ELECTROPHYSIOLOGICAL ANALYSIS OF THE VISUAL SYSTEM IN INSECTS

By H. AUTRUM
Department of Zoology and Comparative Anatomy, University of Wurzburg

No précis of this paper was available at the time of going to press.

At a Joint Meeting with the Linnean Society, held in the Rooms of that Society on 24th October, 1957, under the Chairmanship of Dr. Errol I. White, F.R.S., Vice-President of the Society, the following papers were read.

SPATIAL AND TEMPORAL CRITERIA IN TAXONOMY

By G. THINES

Laboratoire de Zoophysiologie, University de Louvain, Belgium

Starting from the distinction of Fage between taxonomy and systematics, a brief analysis is carried out on the place of systematics in evolution. The role of taxonomy as a technique of identification is then considered and compared with the aims of systematics in its broadest sense. The work of taxonomy is then analysed in some of its structural details. *Quantitative space-criteria* based on descriptive morphology, on geographical differentiation and on Statistical studies are then analysed with regards to specific determination. The value of behavioural criteria is then considered and reasons are exposed which allow to consider them as belonging to the category of *quantitative time-criteria.* A comparison of the practical and theoretical value of these two categories is then carried out in the light of some studies of comparative ethology.

SOME RESULTS OF GEOGRAPHICAL ISOLATION IN CLETHRIONOMYS

By J. GODFREY

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Individuals from several geographically distinct populations of bank voles have a range of behaviour patterns which can be predicted, usually quantitatively, from their place of origin.

There is, in the laboratory, partial sexual isolation between these voles. It will be argued that natural selection would tend to improve this barrier if the populations should again become sympatric.

THE BEHAVIOUR AND PHYLOGENY OF THE WEAVER BIRD (PLOCEINAE)

By J. H. CROOK

Department of Zoology, Cambridge

Some ten months field research on the Ploceinae of British and French West Africa has yielded sufficient behavioural data to permit a consideration of its implications for the phylogeny of the group. The species are first classified ecologically into five groups and then, following a discussion of the relative importance of different kinds of behavioural data to systematics, studies of nest form and construction and nest advertisement displays are shown to be of use in species diagnosis. Pair formation, which falls into three categories and territorial behaviour of four types may be used in placing the genera in groups of apparent phylogenetic affinity.

Four such groups are presented in a dendrogram in which the principle division depends upon the retention of the "globular" nest form in *Quelea, Euplectes* and a number of other savannah and grassland species. A simple form of nest invitation display correlates with this. In the other groups inverted nests are found correlating with nest advertisement displays that are given in the "hanging" position with the birds head below the entrance of the nest. Variations on this theme are discussed and it is noted that in each of the groups a trend towards the formation of breeding colonies may be found. Evidence for divergence and convergence of certain species is presented and the probable origin of the present Ploceine avifauna from steppe-adapted forms entering Africa from the north during the Pliocine is discussed.

THE EVOLUTION OF PROTECTIVE DISPLAYS IN SATURNIOID MOTHS

By A. D. BLEST
Department of Zoology, University College, London

(*This précis also covers the paper presented at the Meeting of 21st and 22nd March*, 1957).

Saturnioid moths perform protective displays when disturbed from rest. The displays of 40 Old and New World species have been described; they show a close correlation with the modes of protective colouration, distinct and clearly defined motor patterns being associated with particular types of morphological pattern. Thus moths with detailed procryptic resemblances to dead foliage are strikingly inert to quite violent tactile disturbance, those with hind-wing eyespots exhibit them, usually by static display postures, while conspicuous but non-distasteful moths, and aposematic and pseudaposematic moths each have characteristic types of display behaviour.

Since these displays must have been evolved in response to environmental selection pressures, it might be expected that convergence would be extreme. This is, in fact, the case, and displays whose motor patterns are wholly or nearly indistinguishable are to be found independently evolved in each of the three main families investigated, (Saturniidae, Hemileucidae, and Syssphingidae). They are, therefore, of little use as taxonomic characters, but this is not true of all the behaviour characters of the Saturnioidea, for in many cases such patterns as cocoon-spinning behaviour, and settling movements may be highly conservative and common to whole families or large generic groups.

PROCEEDINGS OF THE SECTION ON ANIMAL BEHAVIOUR AND SOCIOBIOLOGY OF THE ECOLOGICAL SOCIETY OF AMERICA

An afternoon programme of invited papers on *Sexual Behaviour* was held in conjunction with the one hundred twenty-fourth meeting of the American Association for the Advancement of Science in Indianapolis, Indiana, on 29th December, 1957. J. T. Emlen, University of Wisconsin, was in the chair. Abstracts of the papers are presented below.

THE DEVELOPMENT OF SEXUAL BEHAVIOUR

By EVELYN SHAW
American Museum of Natural Science

Sexual behaviour in the adult is defined as an organised sequential pattern of events. Little is known of the development, order of appearance and frequency of these events in fishes, amphibia, reptiles and birds. However, it is known that some mammals execute sexual-like responses long before maturity.

Two factors which are influential in the development of sexual behaviour are hormones and external environmental conditions. Precocious sexual maturity may be induced by hormone injection. Hormone deprivation results in lowered sexual activity. Restricted early environments, in which preceptual opportunities and contact with species mates are reduced, results in lowered sexual activity in many adults.

Our present knowledge leaves us with no concrete conclusions. We need objective studies of the motor development of the organism, further correlation between physiological and behavioural changes and a standardised analytical methodology so that work of individual investigators can be compared.

ENDOCRINE CONTROL OF SEXUAL BEHAVIOUR

By ADAM ANTHONY
Pennsylvania State University

This paper reviewed current ideas regarding direct and indirect hormonal regulation of sex behaviour in mammals. Available evidence indicates that the basic neural components of sex behaviour have a genetic basis which is common to both sexes. Gonadal hormones and experience facilitate, in some unknown fashion, the translation of this pre-determined behavioural repertoire into expression. Gaps in our understanding of endocrine-sex behaviour interactions include: (1) the role of fœtal-hormones in neural maturation; (2) influence of adrenals or thyroids on the responsiveness of tissues mediating sex behaviour; and (3) the dependence of endocrine action on genetic constitution, perceptual stimuli and CNS regulatory factors schematically summarised in Figure 1 (not reproduced here.)

Comparative studies of endocrine-sex behaviour interactions in other species, particularly seasonal breeders, should provide a more comprehensive picture of the dependence of mating on sex hormones and experience. This is apparent when one realises that much of our present knowledge is based on work with laboratory rodents which represent less than two per cent. of the available native species.

STIMULUS CONTROL OF SEXUAL BEHAVIOUR

By E. B. HALE
Pennsylvania State University

Data obtained with male turkeys (in co-operation with M. W. Schein) and with bulls (in co-operation with J. O. Almquist) serve to illustrate several aspects of the stimulus control of sexual responses.

Experiments using a dummy female turkey with detachable head confirmed observations with live females that the head serves as a directing stimulus by which the male achieves proper anterior-posterior orientation. Placing the head at positions other than the normal one consistently led to disorientated copulatory movements.

Male turkeys presented a body without the head displayed but did not mount. Presenting the head alone (upright) released display behaviour followed by "mounting" and copulatory movements immediately posterior to the head. A three-week old poult injected with male hormone reacted similarly to the head of a dummy poult.

The role of novel stimuli in initiating sexual responses has been investigated with dairy bulls. Sexual satiation to one stimulus animal did not reduce responsiveness (ejaculations) to new stimulus animals. Response to new animals was immediate with gradual decrease in responsiveness in the presence of the constant stimulus Recovery of responsiveness to a specific stimulus. animal one week after satiation ranged from slight to complete, with the percentage recovery unrelated to the initial response level. Reaction time to a constant stimulus animal was reduced markedly by presentation in a new location. For example, presenting the stimulus animal 3 feet to the rear of the usual location reduced reaction time to 20 per cent. of the previous level. A series of tests measuring initial response, recovery of stimulus specific responses, and responsiveness to new stimulus animals indicated that these are three independent aspects of sexual behaviour.

Sexual satiation is interpreted as specific to the stimulus in a specific situation (within the limits of stimulus generalisation). This conclusion has several theoretical implications.

INDUCED SEXUAL RESPONSES BY INTRACRANIAL CHEMICAL STIMULATION

By ALAN FISHER
University of Pittsburgh

Utilising a technique permitting direct chemical stimulation of local brain areas in freely moving animals, findings related to sexual behaviour and its neural correlates have been forthcoming. Minute, localised introduction of hormone salts to specific brain loci has elicited heterosexual behaviour in male and female rats, hypersexuality in males, and male sexual behaviour in females.

Complete sequences of male sex behaviour have been elicited, including ejaculation without penetration into the vagina. The data bear directly on current theories of sexual mechanisms and the role of hormones in behaviour.

Integrated behaviour has been elicited only following stimulation with specific chemicals at specific brain loci. In respect of sexual behaviour, the data favour a "neural centre" theory, in which a selectively sensitive cell area within a sensory-motor system may block, select or integrate patterns of neural impulses, depending in large part on the level of a critical chemical action.

Testing of control compounds has revealed only one giving results equivalent to those obtained with soluble hormone salts. The compound, Versine, is a chelating agent, and further study may relate the metallic-ion removal action of the chelating compounds to the unknown mechanism of hormone action.

COMPARATIVE STUDIES OF SEXUAL BEHAVIOUR

By JOHN A. KING

R. B. Jackson Memorial Laboratory, Bar Harbor, Maine

Comparative studies of sexual behaviour may be made among animals with differences in the number of common genes they possess. Comparative studies based upon these genetic differences were placed into three categories: (1) *genetic comparisons*, (2) *specific comparisons*, and (3) *phyletic comparisons*. Each category of comparison employs different techniques and enables the investigator to draw conclusions particular to that category.

Genetic comparisons are made among animals with relatively similar genotypes, such as single gene differences (mutant strains), or multiple gene differences (individuals, litters, breeds, races, selected and inbred strains). Animals with these genetic differences are capable of interbreeding and thus provide material for genetic analysis. Studies at this level demonstrate the genetic contribution to patterns of sexual behaviour, usually through physiological mechanisms.

Specific comparisons are made among species of animals in which the genetic differences are usually great enough to reproductively isolate them from each other. Studies of several different species often reveal homologous patterns of sexual behaviour and thus provide evidence for their evolution.

Phyletic comparisons between animals which differ at the familial, ordinal or class taxonomic levels have very few common genes and, therefore, rarely reveal evolutionary sequences of behavioural paterns. Such studies, however, contribute to our knowledge of basic neurological and physiological processes of animals at different phylogenetic levels.

Each of these three types of comparison were illustrated by experiments selected from the literature to demonstrate the techniques used and kind of conclusions drawn.

CORRESPONDENCE

Incubation and Clutch Size in Gulls

SIR,

Paludan (1951) and Weidmann (1956) presented extremely interesting data on the termination of laying in gulls, from which it was apparent that the Black-headed gull (*Larus ridibundus*), the Herring Gull (*L. argentatus*) and the Lesser Black-backed Gull (*L. fuscus*) are indeterminate layers. If the eggs were removed within 12 hours after laying, additional eggs would be laid at normal intervals. As supporting evidence, a few female birds were killed during the laying season and more than three stalked follicles were found in their ovaries: three is the normal clutch size. However, if the first egg was left in the nest and the subsequent two were removed, additional eggs were not laid. It therefore seems that the end of laying is correlated not with a definite number of eggs in the nest, but with opportunity for the bird to incubate. Weidmann concluded that incubation has an inhibitory influence on the growth of follicles, and that this limits the number of eggs to be laid after the gull has begun to sit.

As these authors did not attempt to relate their findings to available endocrinological information, I shall try to do this. There is evidence that in the hen (Saeki & Tanabe, 1955), the pigeon (Lahr & Riddle, 1938; Schooley & Riddle, 1938) and also, by good fortune, in the California Gull, *Larus californicus* (Bailey, 1952), there is a high level of prolactin secretion by the anterior pituitary during incubation. There is much evidence in various birds that prolactin has an inhibitory effect upon the gonads in both male and female, and in particular that prolactin treatment inhibits the growth of ovarian follicles and suppresses laying (Bates, Riddle & Lahr, 1937; Lofts & Marshall, 1956; see also Sturkie, 1954; Marshall, 1955; Breneman, 1955). This is thought to be an indirect effect via an influence on gonadotrophin secretion, but this is not yet adequately proved. Thus, it is reasonable to suppose that if there were a rise in prolactin secretion at the beginning of incubation this could, directly or indirectly, terminate laying.

Saeki & Tanabe (1955) showed in the hen that continued incubation of eggs can maintain a high prolactin potency of the pituitary, and Patel (1936) gave evidence suggesting the same in pigeons. Riddle & Lahr (1944) treated ring doves which had been provided with eggs with a variety of agents other than prolactin. After some of these treatments the birds began to incubate, and after the normal incubation period their crops produced milk, which is known to be a direct response to prolactin. It was therefore concluded that the effective agents stimulated prolactin secretion, which then caused the birds to incubate. Although the actual results are of considerable interest, this interpretation seems invalid. There is no evidence that the effective agents used by Riddle & Lahr, 1944 (viz. progesterone, testosterone and desoxycorticosterone) do in fact stimulate prolactin secretion in the absence of eggs (Meites & Turner, 1947). Further, Lahr & Riddle (1944) showed that these agents had various differing effects upon the dove testis, which were mostly not comparable with that of prolactin. Lehrman (1958, and unpublished) has recently repeated and extended these investigations and has concluded that it is progesterone (which Riddle & Lahr found highly effective) which induces the doves to incubate, while prolactin is altogether ineffective at doses consistent with the normal state of the crop at the onset of incubation. The inference therefore to be drawn from Riddle & Lahr's experiment is that the act of incubation, or stimuli received thereby, stimulates prolactin secretion. This is in agreement with Patel's findings and with those of Saeki & Tanabe, and admirably fits the information obtained by Paludan and Weidmann on gulls. It therefore seems probable that the onset of incubation in the gulls leads to increased prolactin secretion by the pituitary which, in turn, leads to the termination of laying.

I am extremely grateful to Dr. D. S. Lehrman for his comments and the permission to use his unpublished material.

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BOOK REVIEWS

Evolutionary Theory and Christian Belief. By DAVID LACK, F.R.S. London: Methuen. Pp. 128. 10s. 6d.

The theory of evolution has always been a scientific cat amongst the theological pigeons and Dr. Lack is only the latest to point out that however peacefully pussy may sometimes seem to sleep among apparently habituated birds, there is a basic incompatibility between avian and feline nature. In his last chapter he sums up earlier ones (themselves summaries of over a century of inconclusive battles on many fronts), with the outcome still in balance, his admitted aim being to assess Darwinism in relation to theism and atheism, not to plead any cause. Explaining the traditional difficulties of fitting moral values into an evolutionary theory, he makes the point (p. 104) "(the scientist) cannot accept the fact that man's mind was evolved wholly by natural selection if this means . . . that the conclusions of the mind depend ultimately on their survival value and not their truth, thus making all scientific theories, including that of natural selection, untrustworthy." But what if truth is itself the ultimate survival value? What if the real point is not whether ethics can evolve, but that they must, or bust?

Lack reminds us (p. 99) that T. H. Huxley could not explain how the cosmic process could give rise to a system of ethics opposed to it; but ethics need not be so opposed if they get into the main stream of life and thus become free to evolve as part of it. At present they are out on a limb, and that way lies extinction, As Sherrington puts it (*Man on his nature* 1940): "What are the most successful individuals which life has to show? The multicellular . . . (yet) multicellular organisation is in itself a variant from the perennial antagonism of cell and cell . . . It is surely more than mere analogy to liken to those small beginnings of multicellular life of millions of years ago the slender beginnings of altruism today."

Elsewhere (p. 97) reminds us that Haldane maintained that science "cannot, of course, give an answer to the question, 'Why should I be good?' " Why should not the answer be "Because I am part of life which depends on me in an indispensable link in the evolutionary chain"? Whether the theologians will let orthodox Christianity follow its master is admittedly a question, but there need be no conflict between evolutionary theory and the Christ who said "I am come that they may have life, and may have it more abundantly."

E.M.B.

Learning and Instinct in Animals. By W. H. THORPE. London: Methuen. 1956. Pp. 493. 9 plates. 55s.

In recent years students of behaviour have been split into two camps: one, comprising the European ethologists, has been primarily concerned with the analysis of instinctive behaviour, while the other, consisting of a number of diverse schools of experimental psychology centred in the United States, has tended to concentrate

on the study of learning processes to the exclusion of unlearnt behaviour, sometimes going so far as to deny that the latter is anything more than an experimental artefact. Dr. Thorpe's book "Learning and Instinct" is a noble attempt to bridge the gulf between these two methods of approach, and it may be said at the outset that his task is as important for the future of behaviour studies as it is difficult of achievement; for the author of any such enterprise must effect a union between two still adolescent disciplines, one with a reputation for charming naïveté, the other for a precocious and often spurious sophistication.

The present work offers three main themes: firstly, Dr. Thorpe is much concerned with the meaning of the term "purpose", and with "purposive" behaviour. Secondly, he has compiled an immense volume of data bearing on the distribution of learning capacity in different Phyla; lastly, in addition to classifying and critically assessing the evidence for different types of learning at the descriptive level of analysis, he has essayed a triple synthesis between modern learning theory, neurophysiological hypothesis, particularly that relating to cybernetic models, and recent ethological concepts of "drive." Inevitably, with so broad a programme, many of the opinions expressed on matters of theory are controversial, and this book must not be taken as representative of the theoretical attitudes of any one school of behaviour study.

Perhaps the least satisfactory chapter is the first, which is titled "Directiveness and Purposiveness." Dr. Thorpe builds upon the extrapolations which W. E. Agar has made from Whitehead's philosphy of organism to conclude that "*the concept of perception includes an actively organising, possibly a purposive, element; and that perception is a basic characteristic of the drive of the living animal.*" A distinction is made between purposiveness and directiveness, and "purpose" is defined as "*a striving after a future goal retained as some kind of image or idea.*" This as a background attitude to the practical business of research is interesting and important, but in assessing it the reader tends to get lost in a maze of inadequately defined terms. The type of analysis attempted by Sommerhoff in "Analytical Biology" is here rejected, but the refutation is neither detailed enough, nor sufficiently closely argued to allow judgment. Many readers will rightly regret this, for the issue is not one which workers in the field of behaviour can afford wholly to ignore. This discussion, however, constitutes but a small part of the entire work, and offers the advantage that the author's metaphysic is firmly separated from his science.

The sections on types of learning and their possible mechanisms collate a wide range of material and contain numerous stimulating juxtapositions. Instinctive behaviour is regarded as being a later evolutionary derivative of primitive learning capacities, and there is a chapter dealing with hypothetical systems capable of learning, based on neurological and mathematical models.

The last and longest part of the book, which deals with the learning abilities of the main groups of the animal kingdom, will undoubtedly be an indispensable source of reference for many years to come. The expositions are clear, and comprehensive accounts of the present states of a number of fields of research, including sections on arthropod behaviour, homing, migration, neurological studies of learning in invertebrates, and the work of the author and his colleagues on the rôles of instinct and learning in the acquisition of song-patterns by young passerines. The authors whose work is thus summarised will have reason to feel that they have been justly treated. It is, nevertheless, a sign of the rapidity with which the subject is expanding, that a number of important papers on topics which include the ontogeny of behaviour, honey-bee communication, and diurnal rhythms have been published since the book went to press. As it will certainly become an important and probably unique text for zoological students of behaviour, it is to be hoped that it will prove possible to incorporate additions and revisions as they become necessary into future editions.

A.D.B.

BOOKS RECEIVED

The following books have been received and in appropriate cases will be reviewed as space permits in early issues.

A. & S. Bell (1956)
Some Common Australian Birds
Oxford University Press 35s.

C. Hume (1957)
Skunks as Pets
Wisconsin: All Pets Books Inc. 75 cents.

On the Dynamics of Exploited Fish Populations

By R. J. H. Beverton and S. J. Holt

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3 · 4

BEHAVIOURAL EVIDENCE ON THE EVOLUTION OF BATESIAN MIMICRY

By ROBERT S. SCHMIDT
Illinois State Normal University, Normal

Introduction

A good deal has been written about mimcry and its evolution. Cott (1940) reviews the evidence showing that although the status of some specific cases may still be in question, the existence and adaptive value of mimicry and other forms of protective coloration can no longer be seriously questioned. Goldschmidt (1945), Ford (1953), and Cott (1940) discuss some of the theories that have been advanced to explain the evolution of mimicry. Only two of these theories seem to receive much support today and our attention will be limited to them.

The Neo-Darwinian or Micromutation theory assumes that mimetic resemblances have evolved in a manner similar to that of other types of adaptations—i.e. by the gradual accumulation of small mutations with an accompanying change from a slight to an increasingly complete resemblance to the model.

The Saltation or Macromutation theory has been used by the macroevolutionists as one of the lines of evidence supposedly supporting their views (Goldschmidt, 1945). (See Goldschmidt, 1952, for a recent review of his concepts of macroevolution and macromutation.) This theory supposes that the resemblance cannot have evolved in small steps, because a slight resemblance would not provide a mimic with a similarity close enough to the model to deceive its enemies. In this case the increased conspicuousness might actually be detrimental. Therefore, origin of a more or less complete resemblance through a single macromutation is considered *essential*. "If our two species, model and would-be mimic are, to begin with, markedly different in pattern, how can we suppose that a slight variation in the direction of the model on the part of the latter would be of any value to it?" (Punnett, 1915, p. 62). "The Neo-Darwinian theory cannot work. . . . before a resemblance of the mimic to the model is established which is at least so close that the predators are deceived, even if the similarity is not yet perfect" (Goldschmidt, 1945, p. 162).

Most of the discussions concerning the validity of these two theories have been based upon genetics, with the most general acceptance going to the Neo-Darwinian theory (e.g. Ford, 1953). With few exceptions (e.g. Carter, 1946, 1948; Cott, 1954), one line of evidence—the behaviour of the predator—has not been utilised to any extent. Most experiments in the field of mimicry deal not at all or only indirectly with the degree of resemblance needed to deceive a predator. No theory of the evolution of mimicry can be complete without accurate knowledge on this point, since it is the predator that provides the selection pressure directing the origin of mimetic resemblances. Both theories have been based to a large extent upon unproven assumptions about predator behaviour—one theory assuming a slight resemblance to be effective while the other assumes a complete resemblance necessary to cause deception. The test of these two theories is thus as much in the realm of animal behaviour as it is in the realm of genetics and evolution.

Therefore, the purpose of this paper is to shed light upon the question, "is a small resemblance to a model sufficient to provide a selective advantage to an incipient mimic?" The discussion will be limited to *Batesian* mimicry, since the Saltation theory does not seem to have been specifically extended to Müllerian mimicry or other types of protective coloration. The discussion will also be restricted to the more complex forms of Batesian mimicry (such as are found among the butterflies), for it is here that the two theories differ most. In smaller insects the size alone would limit the complexity of shape, pattern, and colour of a model to such an extent that even a "small" resemblance, in terms of the microevolutionists, might be very close to the "complete" resemblance required by the macroevolutionists.

Method

A number of day-old White Leghorn male chicks and a few week-old females were bought

from a local hatchery. These were presented with the following three types of life-sized drawings (made with India ink and coloured pencils) on 4 × 5 filing cards:

1. *Model.* A hypothetical butterfly (Fig. 1).

2. *Mimics.* Hypothetical butterflies of various shapes, sizes, colours, and patterns (Fig. 1).

3. *Non-mimics.* A variety of insects sufficiently different from the model that any resemblance would not be likely. The colours used were largely black, brown, and green with some white and yellow. These included 5 Coleoptera, 3 Diptera, 1 Ephemerida, 2 Hemiptera, 2 Homoptera, 4 Lepidoptera, 1 Odonata, 2 Orthoptera.

Each chick was trained to avoid the model. After the first few training periods, it became obvious that time would not permit the use of all specimens. All but four chicks (3 males and 1 female) were therefore destroyed. The four retained were those showing the greatest degree of learning. However, none of the chicks had learned to avoid the model to any great extent by the time the majority were eliminated. Before finally learning to avoid the model, the chicks used for the experiment gave some poorer responses than had some of the other chicks before being destroyed. It is therefore very unlikely that any selection for intelligence resulted from this elimination.

Training was started at five weeks of age for the female and at four weeks for the males. In training, each chick (after being starved from 3.5 to 10 hrs.) was presented with a drawing through a window at the end of a training box. A light behind the drawing was the only source of illumination in the room. Under the drawing was a small food dish containing yellow cornmeal. During presentation of the model, food mixed with a small amount of potassium hydroxide was used. The KOH was kept in a dessicator until needed. The amount of KOH was kept just high enough to produce a pronounced reaction (head-shaking or bill-wiping) if eaten, but low enough so as not to prevent further interest in feeding. An average of 2.2 non-mimics were presented between each presentation of a model. The exact number of non-mimics between any two consecutive model presentations was determined by the readiness of the chick to respond to non-mimics. That is, whenever a chick began to show prolonged hesitation before feeding during presentation of non-mimics, the proportion of non-mimic to model presentations was increased. Non-mimics were chosen at random. Here, as in the experimental periods, the chick was immediately pushed from the food dish (if it fed) or separated from the food (if it did not feed within twenty seconds) by a cardboard partition. The partition was then removed after first changing drawings.

The model was presented 2-17 (average 6.2) times in any one training period. The number of complete avoidances to the model, incomplete avoidances plus nonavoidances to the model, and non-mimic presentations were recorded for each chick. Complete avoidance was taken as failure to feed for twenty seconds. To determine whether any learning of some visible characteristic of food with KOH had taken place, edible food was occasionally presented with the model. Two model drawings were used alternately to prevent learning of irrelevant clues not associated with the model itself.

Chick I received 11 training periods covering ten days and the model was completely avoided 26 of 27 times during the last 5 periods. Chick II received 18 training periods covering seventeen days and the model was completely avoided 28 of 31 times during the last 5 periods. Chick III received 13 training periods covering eleven days and the model was completely avoided 37 of 39 times during the last 7 periods. Chick IV received 13 training periods covering twelve days and the model was completely avoided 30 of 30 times during the last 6 periods.

The details of the training periods were not recorded or studied for two reasons. First, mimicry can be considered an established phenomenon. Therefore, the only purpose of the training period was to produce avoidance to the model as simply as possible in preparation for the experimental periods to follow. Second, detailed study of the training period would have told little about the rate of learning to avoid a model under natural conditions. For instance, other types of studies using actual insects (e.g. Mostler, 1935) show much more rapid learning (sometimes after one experience) than was obtained here. One reason for this difference might be that here the chicks not only had to learn *what* pattern to avoid, but *first* had to learn to associate the patterns with the food. Another possible reason is that punishment for a wrong response may often be much more severe and more prolonged under conditions in the field.

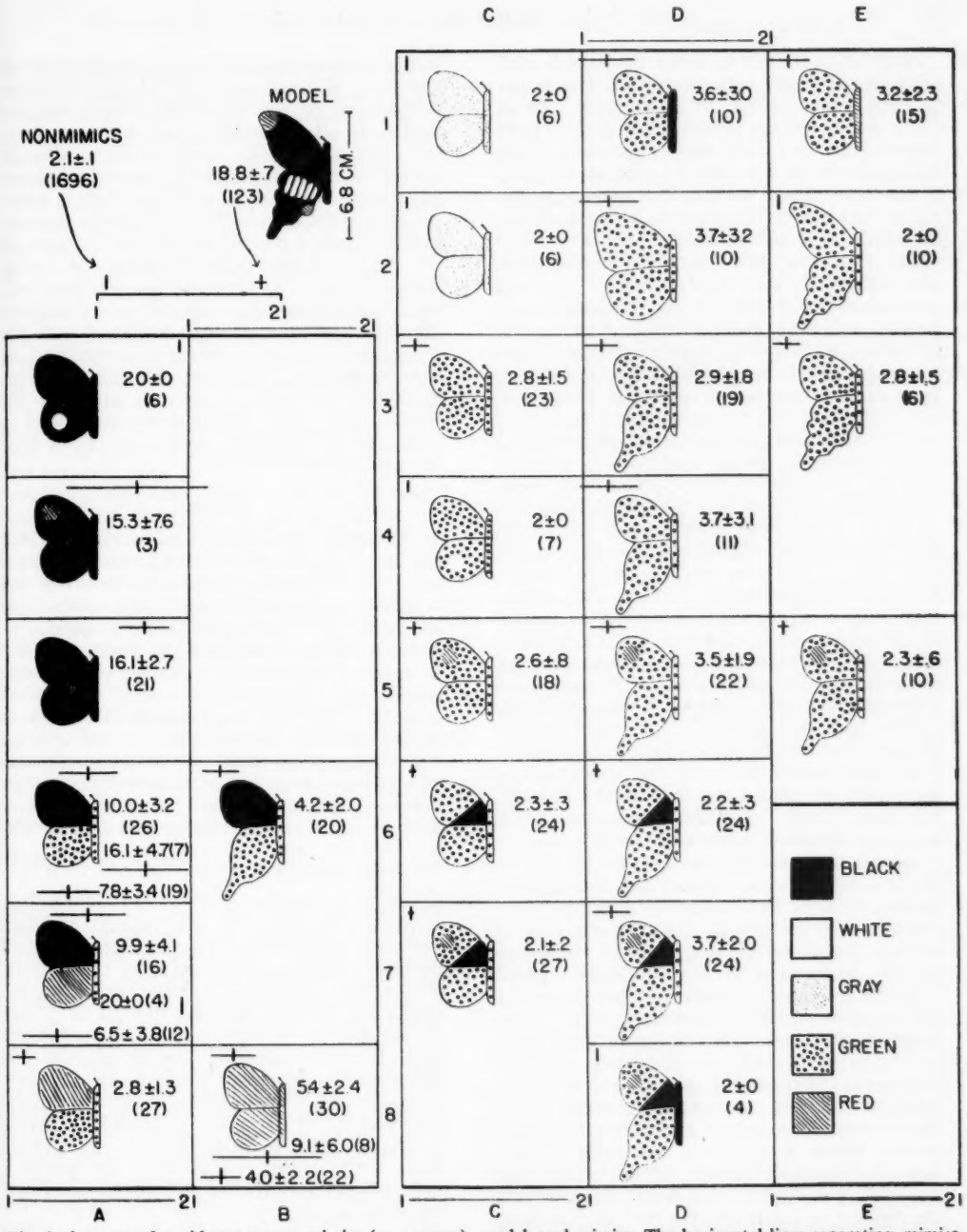

Fig. 1. Amount of avoidance to non-mimics (as a group), model, and mimics. The horizontal lines separating mimics serve as a scale from 1-21 seconds. The mean seconds of avoidance is indicated by the vertical line above each figure. Horizontal lines extend from the mean plus and minus twice the standard deviation of the mean. The responses for all chicks have been pooled in each case. The exact data is given beside each mimic. The total number of responses from all chicks to a mimic is indicated in parenthesis. For mimics 6A, 7A, and 8B the data for one chick (first graph below the mimic) is graphed separately from the other three (second graph below the mimic). All drawings are to the same scale.

After being trained to avoid the model, each chick was presented with the mimics. This began at eight weeks of age for the female and at seven weeks for the males. New mimics were prepared as their need was suggested by preceding results. In the case of a number of these, it was immediately obvious from observing the chicks that new information (not already being obtained from other mimics) was not being found and they were therefore discontinued. This explains the very small number of responses to some of the mimics in Fig. 1. Each experimental period was preceded by a short time of starvation, as before the training periods. There was not more than one period per day, no more than 10 mimics were presented per period, and no mimic was presented more than once during any period. The model was presented 1-4 times (usually 2) during each period. The first two presentations of each period were non-mimics and the third was the model. This was to make certain that avoidance of the model had been retained. The model was also usually presented at the very end as reinforcement. During the experimental periods, only edible food was used, with the following exception. On those few occasions where a chick failed to give complete avoidance to the model, the next presentation of the model was often accompanied with KOH-food in case of another avoidance failure. At least three non-mimics were inserted between any two adjacent mimic presentations. Four non-mimics followed any mimic giving incomplete avoidance (less than twenty seconds). Five non-mimics followed any complete avoidance to a mimic or presentation of the model.

Each chick was allowed twenty seconds to make a response to a mimic. After each presentation, the time from removal of the partition until feeding (if this occurred at all) was recorded (indicating the intensity of avoidance) as well as whether or not the chick showed signs of hesitation. Hesitation was shown by one or more of the following: sustained visual fixation directly upon the drawing, a "surprised" or "angry" squawk, head-shaking or bill-wiping (as though it had taken a bite of KOH-food), excitement, tearing of the paper lining the bottom of the box, or retreat to an opposite corner where it paced or sat quietly. Such hesitation would seem to clearly indicate that the bird was "disturbed" by the pattern. In the absence of hesitation, the bird went directly to the food (usually within 2-3 seconds) and fed rapidly. A response to a drawing was considered as some degree of avoidance only if it was accompanied by some of the indications of hesitation. If avoidance occurred, the time until feeding (up to the 20 second limit) was recorded. In all cases this exceeded two seconds. All other responses (not showing definite hesitation) were considered as 2 second responses (regardless of actual reaction time) when calculating the data in Fig. 1. This was done so that any delays due merely to such factors as low degree of starvation or facing the wrong end of the box when the partition was removed, would not appear as avoidances. It is also possible that some cases of slight hesitation were not recognised and were therefore considered as non-avoidances. Thus any subjective errors in classifying responses do not prejudice the results, since they would have introduced a bias *against* rather than in favour of the conclusions discussed below.

Results

The results are summarised in Fig. 1. There the mean seconds of avoidance (plus or minus twice the estimated standard deviation of the sample mean) to each mimic, the model, and the non-mimics (as a group) are graphed. The mean avoidance produced by a drawing was determined by totalling avoidance times for all chicks and dividing by the total number of responses. This pooling of responses from all chicks was done because evolution of a mimic would take place under the selection pressure of a *population* of predators rather than of an *individual* predator. The estimated standard deviation of the sample mean was derived with the formula: $\hat{\sigma}_{\bar{x}} = \frac{S_x}{\sqrt{N}}$ where x is the mean seconds of avoidance; N is the number of responses, and Sx is the sample standard deviation. In Fig. 1, twice the estimated standard deviation of the mean is used as an approximate 95 per cent. confidence band in estimating the theoretical population mean typical of a particular pattern. The greatest amount of avoidance possible would be twenty seconds and complete non-avoidance would be two seconds. This method of treating the data was chosen, first because it permitted assigning a specific avoidance value to each pattern; and second, because the value could then be graphed, permitting visual grouping and comparison of the different patterns.

There is no statistically significant avoidance of any of the mimics in the last three columns of Fig. 1 when they are compared with responses

to non-mimics. It is possible that a larger number of responses might have shown slight avoidance in some cases. However, since no substantial avoidance is shown by this data, these patterns will be assumed to give no "protection" to their mimics.

On the other hand, the mimics in the first two columns of Fig. 1 (except 8A) show statistically and probably biologically, significant avoidances when compared with non-mimics.

Comparison of mimics in the last three columns of Fig. 1 with each other and with the non-mimics shows that, within the limits of this experiment, there was no significant avoidance to: shape or size (e.g. compare 3C, 3D, 3E, 2E, 2D, and non-mimics), green or grey (e.g. compare 3C, 2E, 2C, and non-mimics), white spot (e.g. compare 3C, 4C, 3D, 4D, 2C, 1C, and non-mimics).

A sufficiently large area of red caused avoidance (e.g. avoidance to 8B but not of 1E, 5C, 5D, or 8A), as did a sufficiently large area of black (e.g. avoidance of 5A, 6A, 7A, and 6B but not of 1D, 6C, or 6D). There seems to be a threshold below which there is no avoidance.

In spite of the various combinations of pattern, colour, size, and shape shown in Fig. 1, there seems to be no evidence for any type of summation effect resulting in significantly increased avoidance from combining different factors. Possible reasons for this will be discussed in the Conclusions. However, there is evidence for increased avoidance with changes in a single characteristic. Increase in area of black (compare 6A and 7A with 5A) or increase in proportion of black (compare 6B, 6A, and 5A) results in increased avoidance.

As might be expected, no two chicks responded in precisely the same manner. No obvious differences were noted in the mimics in the last three columns of Fig. 1., since here there were very few avoidances by any bird. However, differences did show up to mimics causing significant avoidance. These differences were most obvious in mimics 8B, 7A, and 6A. In these instances, the data for one chick (a male) was graphed separately from the other three (Fig. 1). The difference in 8B is not statistically significant but probably would have been if the one chick had not learned *not* to avoid the mimic, since three of the first four presentations to this chick gave complete avoidance.

There is considerable evidence that continued experience with a particular mimic resulted in learning not to avoid that mimic or at least in decreased avoidance. Fig. 2 shows the responses chronologically for several chicks to several mimics. The tendency toward decreased avoidance is obvious. A similar effect was even noted in the data for mimics giving no significant avoidance. Of the 15 avoidance responses (greater than five seconds) to mimics in the last three columns of Fig. 1 and mimic 8A, 13 (86.66 per cent.) were given during the first third of the presentations. Of course, only 33.33 per cent. would have been expected during the first third presentations if the degree of avoidance had remained constant. One of the two responses not falling in the first third was in the first half.

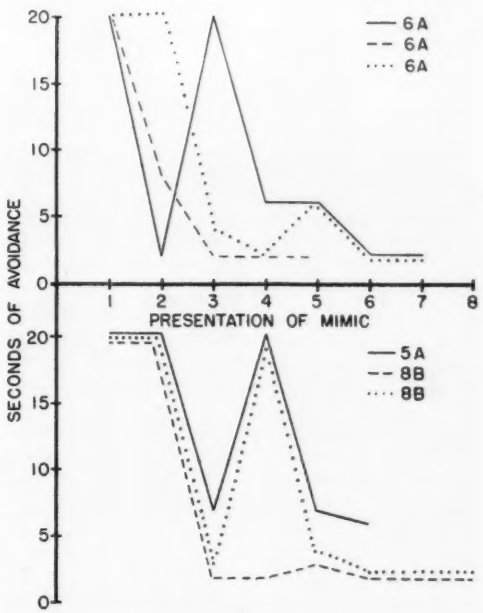

Fig. 2. The decrease of avoidance with increased exposure to a mimic. Numbers and letters (5A, 6A, and 8B) represent mimics in figure 1. The responses of several chicks are shown in the case of mimics 6A and 8B. X axis shows responses in chronological order. Y axis shows length of avoidance in seconds.

Conclusions and Discussion

Degree of Resemblance Needed for Protection

Within the limits of this experiment, the original question has been answered—*a very incomplete resemblance will cause avoidance.*

The validity of the experiment might thus be discussed. There are a number of differences from natural conditions. The "insects" were separate from the food and source of punishment. The main effect of this was probably to prolong the time needed to learn to avoid the model. Punishment may have been less severe and less prolonged than usual under natural conditions. Of course, the birds were limited in number and were not a wild species. The frequency of exposure to model and mimics was certainly greater than in the field. This was probably the main cause of learning not to avoid some of the mimics originally avoided. The interval between exposures to model and mimic and between mimics was much shorter than normal. The stimuli used were not living insects. The conditions of observation were such that the birds probably got a better view of the patterns than would often be expected in the field. There was no movement of the "insects"; there was plenty of light; there was no interference from shadows, background, or cover; and there were no obvious distractions.

In spite of these differences, this type of experiment had some obvious advantages. The situation could be controlled to a degree that would be impossible in a more natural situation. The animals used were naïve, having had no previous experience with insects. Fairly detailed and accurate observations of the behaviour of the responding birds were possible. Since the main purpose was to study response to mimics after training against a model, and since both mimics and model were used under similar conditions, it can probably be assumed that the results for these chicks would have been similar qualitatively (but somewhat different quantitatively) under more natural conditions. That is, the same mimics would probably have given the greatest avoidances, although the exact intensity of avoidance might have been different (probably greater?).

Some of the evidence suggests very strongly that avoidance to mimics would have been greater under natural conditions. As has been noted, there was some learning *not* to avoid mimics. This lowered both the mean avoidance and its standard deviation. This may well have been due to the fact that the birds saw each mimic so frequently. In the field, a mimic (and especially an incipient mimic) would have been found so rarely by any one bird that such learning not to avoid would not be likely to occur. Also, a bird in these experiments had only the choice of feeding or not feeding. A bird in the field would have had the additional possibility of looking for other food. Under such conditions it might have been less "inclined" to "take a chance" on a "questionable" insect. Starvation before the experimental periods had to be great enough to induce prompt responses. It is possible that under normal field conditions the average degree of satiation may often be greater, thus making the bird less likely to respond to insects of "questionable" edibility. For instance, Marler (1955, p. 116) found in the chaffinch that "the effect of starvation is to increase the tendency of birds to approach a seed dish, whether or not it is already occupied by a dominant bird. . . . . Thus it appears that starvation reduces responses to escape stimuli in general, not merely those emanating from a food source."

A good deal of indirect evidence on the subject is in the literature of animal behaviour. In fact, if an *a priori* assumption were to be made concerning the behaviour of predators involved in the evolution of mimicry, one would have to suppose that a small resemblance could be effective in causing avoidance. There is certainly no evidence to support the conclusion of Punnett (1915, pp. 81, 83) that:

> Really we can do little more than to describe how these mimetic resemblances appear to our own seness, and to infer that they do not appear very different to the bird. . . . My experience was that whether at rest or flying the species are perfectly distinct, and I find it difficult to imagine a bird whose living depended in part upon its ability to discriminate between the different forms would be likely to be misled. Certainly it would not be if its powers of discrimination were equal to those of an ordinary civilised man.

Goldschmidt's (1945, p. 162) conclusions are similarly naïve:

> Can we really assume that the birds and monkeys and also mantids are such wonderful observers (or that some very clever ones among them are) to notice a "remote" resemblance and to be repelled by it? I think that is asking too much. The minimum any selection theory of mimicry needs is a *fair* resemblance. But if we look at the actual specimens we realize that a fair resemblance would be not very much different from the present mimetic pattern.

Almost any comparative anatomy, physiology, or psychology book shows numerous differences in the visual equipment and behaviour of different species. The following quotations are merely a few of those that could be used to illustrate the fallacy of anthropomorphic views of predator behaviour:

> We have discussed the colours as we see them on butterflies and moths, although the colours as butter-

flies and moths see them would probably be more to the point. (Lutz, 1933, p. 566).

In certain circumstances many animals—including birds, lizards, fishes and various invertebrates—recognize objects in a way very different from a human observer. (Cott, 1954, p. 49).

Mimetic resemblances have not evolved under the selection pressure of man. Therefore, the appearance of a mimic or model to us is irrelevant.

The use of models in the study of the behaviour of the stickleback (Tinbergen, 1951), the herring gull chick (Tinbergen, 1955), and the English robin (Lack, 1943) are merely a few examples showing that "an animal does not react to all the changes in the environment which its sense organs can receive, but only to a small part of them" (Tinbergen, 1951). Unfortunately such evidence, although very suggestive, is not conclusive. First, it does not deal directly with complex mimetic patterns. Second, these studies deal not with learned (and avoidance of a model is learned) but with innate behaviour patterns.

Therefore, studies showing equivalence of various patterns to a *learned* pattern from which they differ are of even more direct interest to us. Studies by Lashley (1938) illustrate some visual equivalents in the rat. He trained rats in his jumping apparatus to jump to a positive pattern associated with food while avoiding a negative stimulus associated with a fall. The animals were then presented with pairs of strange patterns. If they gave positive responses to one member of the new pair to a significantly greater degree than to the other, this pattern was considered to be equivalent in some degree to the positive training figure. Fig. 3 illustrates some of these training patterns and some of the figures that were found to be equivalent to them. Lashley states that these experiments show that "the animal reacts to a limited part of the total visual field and disregards variations in the remainder" (p. 154). "In equivalence tests the properties of the figure may be varied through a wide range, so as to destroy any physical identity with the training figure without destroying the reaction" (p. 185). Thorpe (1956) notes that in learning an "animal often appears to select one type of cue, and if he succeeds on this basis will not use the others at all. If, however, he is successful, the less preferred responses are brought into use".

Allee (1952), Lack (1943), and Tinbergen (1951; 1953), among others, note that some

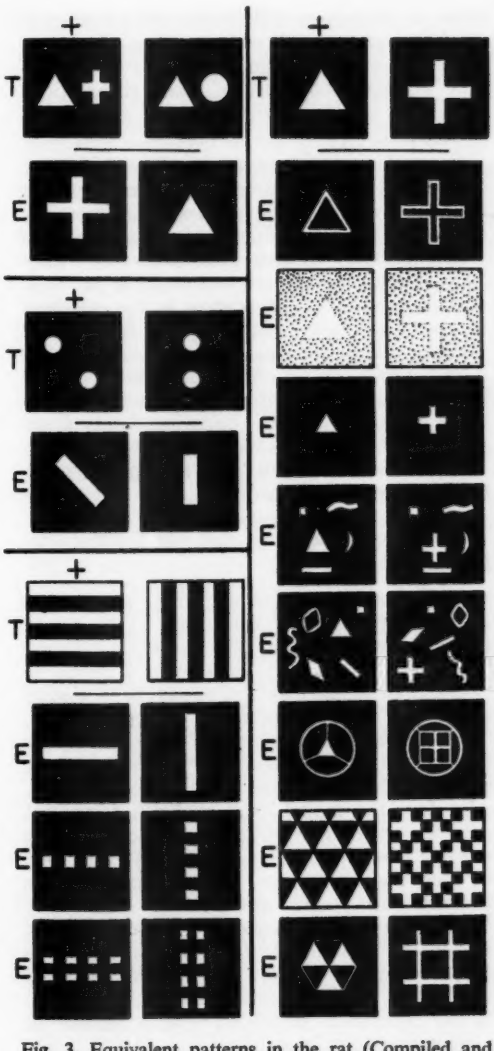

Fig. 3. Equivalent patterns in the rat (Compiled and modified from Lashley, 1938). T=pair of training stimuli (+=positive stimulus). E=pair of stimuli used in equivalence test (left-hand member of each pair equivalent to some degree to positive training stimulus).

animals are able to recognise *individuals* of their own species and sometimes of other species. However, these observations in no way modify the conclusions concerning the recognition of warning or mimetic coloration by a predator. Social behaviour is by no means the

same as predatory behaviour. An animal has more frequent contact with members of its own social group than it does with any individual prey animals and most of these recognitions require a certain length of time to become established.

From the experiment described in this paper and the abundant indirect evidence from the literature, it may be concluded with fair certainty that a *complete resemblance* of mimic to model *is not necessary* to give some degree of avoidance. It must be remembered that 100 per cent. effectiveness of an adaptation is not required to give a selective advantage. The behavioural evidence alone cannot show that origin of a mimic never occurs by macromutation (the final decision will probably rest with genetics) but it does show that the Saltation theory *is not necessary* to explain the origin of mimicry. The behavioural evidence thus strongly supports the Neo-Darwinian theory.

Type of Resemblance Needed and Further Perfection of Pattern

Resemblance as vague as a *large area* of red or black provided "protection" (Fig. 1). In fact, these were the only characteristics inducing avoidance. Preliminary work with a Monarch (*Danaus archippus*) as the model gave similar results as the experiment described here. The question then arises—if such a simple pattern will give avoidance, why does the mimic evolve such a *complete* resemblance? Indeed, why does the model itself evolve a somewhat *complex* warning coloration? These questions provide the opponents of mimicry with one of their main criticisms. They claim that these patterns are more complicated than they "need" to be and therefore cannot be accounted for on the basis of natural selection. Although these questions cannot as yet be answered completely, and were not specifically dealt with in the experiment described here, a number of explanations are possible.

One feature common to all models, as well as to other types of warning coloration, is their conspicuousness (Cott, 1940). The more conspicuous the model, the more readily will it be learned and recognised by its predators, the more easily will it be distinguished from its surroundings and from other insects, and the greater will be the protection afforded. Added complexity in shape, colour, and pattern may in some cases produce greater conspicuousness than would a bright colour (red) or high contrast (black) alone.

The presence of any Batesian mimics would be likely to exert a selection pressure causing divergence of model pattern (probably by increased complexity) from that of its mimic. Attacks upon the mimics by naïve birds, or occasional attacks by experienced birds would result in decreased avoidance to the models since such attacks would not result in learning to avoid or in reinforcement of avoidance and might even result in learning not to avoid if, for some reason, mimic-predator contacts became too frequent. In the experiment discussed in this paper there was definite learning not to avoid (see Results).

We have already noted that an organism seldom responds to all the visual aspects of the environment. Carter (1946, 1948) has suggested that complex patterns may arise under the accumulated influence of different predators, each responding most strongly to a different aspect of the pattern. Concerning such variability of predator perception, Blest notes that his experiments (1957) "comparing the releasing value for passerines in three different families . . . of three characters present in a two-dimensional eye-like pattern have not supported it, though they offer no positive disproof" (Blest, 1956). However, this is not a just criticism of Carter's suggestion, since Blest's experiments deal with innate behaviour and model avoidance is learned. Although it was not designed specifically with that purpose in mind, the experiment described here shows individual differences between chicks. Some responded more strongly to black than did others, and one avoided red to a much greater extent (mimic 8B Fig. 1). The statistical picture does not adequately show the difference in responses to red, since the one chick eventually learned *not* to avoid red (due apparently to too frequent presentation of the mimic). Thorpe (1951) notes that Mühlmann (1934) also found considerable intraspecific and interspecific variability in response to mealworms (made inedible) with various artificial patterns of red rings. Although much more evidence relating more directly to the problem is needed, it is inconceivable that each individual of each predator species would respond identically to every visual aspect of a warning or mimetic coloration. It would seem then that Carter's suggestion is at least a partial solution to the problem.

It must be remembered that an organism's

predators is not the only influence determining its appearance. Visual stimuli are of at least some importance in the courtship behaviour of at least some butterflies (Tinbergen, 1951; Stride, 1956). It is possible that some of the complexities of a model may be species-specific releasers used in the mating behaviour. If this should prove to be true, then some of the pattern may serve as an isolation mechanism helping to cause and maintain speciation. There may also be other, less obvious, factors selecting various aspects of the pattern.

Explanations of the remarkably complete resemblances of many mimics are also incomplete. It would seem that here, as noted above for the model, Carter's suggestion may account for much of the completeness—different predators selecting different parts of the resemblance.

Even if there were just one type of predator with no variation in model perception, one might expect that any increase in the degree of resemblance of mimic to model would increase avoidance to the mimic and therefore increase its selective advantage. Unfortunately, the experiment in this paper gives very little information on this problem. Increase in either the area or proportion of black seemed to increase avoidance (Fig. 1). However, there was no statistically significant evidence of increased avoidance from combining *different* characteristics. This may very well have been due to absence of the proper type of mimic. Additional mimics with combined features or larger number of responses to the mimics that were used might have given some degree of avoidance. The two characteristics causing avoidance (red and black) seemed to be effective only after their amount exceeded a certain threshold (Fig. 1). None of the mimics not causing avoidance possessed red or black at this level and other features, such as the white spot, may have been present in sub-threshold amounts. It would also seem that any improvement in resemblance would improve chances of survival under suboptimal visual conditions, such as reduced illumination, shadows, cover, or various distractions, under which a predator might not be able to recognise (at least in time to prevent destruction of the mimic) a less complete similarity. Some type of summation effect may therefore be found to account for part of the completeness of mimetic resemblances.

Supposed Method of Origin of a Mimic

Becoming a mimic must be an extremely hazardous process. To acquire an effective mimetic resemblance, an organism must become conspicuous—to become conspicuous brings increased exposure to its predators. The protective effects of the appearance of an incipient mimic must therefore be at least as great as any harmful exposure effects. This and the results summarized in Fig. 1 would suggest strongly that the first effective modification resulting in the formation of an incipient mimic is the addition of a very simple, generalised, but substantial conspicuousness in some feature that is found in the model. A large area of red or black would usually produce this effect. Improvement of the resemblance would then occur through selection of additional mutations. It is highly improbable that the protection provided an incipient mimic even approaches that of its model (except where the model is relatively simple). Indeed, it might be extremely slight. The population size of an incipient mimic would probably have to be even more restricted than that of a more complete Batesian mimic in order to prevent the predator from learning *not* to avoid it due to too frequent contacts. To the knowledge of the author, few, if any, authentic examples of an incipient mimic to a complex model have been collected. It is therefore probable that the evolution of a more or less complete resemblance to a complex model by an incipient mimic may proceed at a rather rapid rate.

It must be emphasized that although the initial modification of appearance may be a "macro"-adaptation in the sense that it is conspicuous, it certainly need not be a *macro*-mutation in the sense of Goldschmidt and his school. The Saltationists imply that the many diverse aspects (pattern, colour, shape, size, behaviour) of a complete resemblance are *all* caused by a single macromutation. Actually the original conspicuous contrast or bright colour would involve only a change in pigmentation and could be very simple genetically.

Preadaptation might sometimes be decisive in getting an incipient mimic past the stage where its conspicuousness may be almost as much a hazard as an asset. It is probable that, at times, the protective effect of a new mutation may be increased by a previously existing pattern having no original relation to warning coloration.

If a mimetic resemblance is to evolve in a species of lepidoptera that depends to any great extent upon visual releasers in its breeding behaviour, the steps in modification of the mimic must not seriously interfere with these releasing aspects of the appearance. Changes in the mating behaviour would be expected to parallel the increase in resemblance to the model. Could this be of importance in the origin of a *single* male form and multiple female forms in some of the polymorphic mimetic butterflies? Perhaps it is the female that recognises the male during pairing, thus giving an advantage to only one male pattern. If interference with mating behaviour should be found to be an important problem faced by many incipient mimics, this would be another blow to the Saltation theory. It would be highly improbable that normal mating behaviour could survive a sudden, radical change in appearance if species-specific visual releasers were impaired.

Summary

1. Four White Leghorn chicks were trained to avoid a drawing of a butterfly (the model) and than presented with various other butterfly drawings (the mimics).

2. Some mimics resembling the model only slightly were avoided.

3. Some of the literature indicating that animals usually respond to only a portion of the visual environment that they are capable of seeing is summarised.

4. On the basis of the experiment and the literature, it is concluded that behavioural studies provide no evidence for and considerable evidence against the Saltation theory and tend to support the Neo-Darwinian theory of the origin of mimicry.

5. Some possible explanations for the complexity of a model warning coloration and the completeness of a mimetic resemblance are discussed.

6. It is suggested that the original resemblance acquired by an incipient mimic is a simple, generalised conspicuousness such as a large area of red or black. This would then be improved by selection of further mutations. The evolution of a more-or-less complete resemblance from the original generalised one may take place very rapidly.

7. The possible importance of preadaptation in the origin of mimicry is suggested.

8. The possibility that in some cases the new incipient resemblance may interfere with releasers involved in breeding behaviour is briefly discussed.

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THE VALUE OF ANIMAL BEHAVIOUR RECORDS IN PASTURE EVALUATION STUDIES

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Until comparatively recently, grassland research has been concentrated on the establishment of grass rather than upon its utilisation by the grazing animal. As a result of the development of specialised strains of grasses and clovers, and the realisation that grassland should be managed as intensively as any other crop, it is now possible to establish good grass fields in most parts of the country, except those subject to prolonged drought. There are still, however, many unsolved problems associated with the utilisation of grassland and the development of methods of evaluating varying pasture types.

Jones (1928) has shown that differences in the nature of swards can be associated with variations in grazing behaviour. He observed differences in the behaviour of sheep grazing on extreme types of herbage, and on a given sward, which was rotationally grazed after varying rest periods. Hodgson (1933) noted that as cattle remained on a restricted area for an increasing number of days, the time spent in grazing lengthened. Later work has been reported by Hancock (1954).

When computing rations for cattle, an allowance of starch equivalent is made to the maintenance portion of the diet to supply the energy used in grazing. Woodman (1954) has suggested that this allowance should vary with sward type. The amount of work involved daily in grazing has been repeatedly stressed by Wallace (1944). Graves, *et al* (1933), using two groups of dairy cattle, have reported that the loss in body weight and the fall in yield were less when cows were fed cut grass indoors than when the same herbage was grazed "in situ". This variation was related to a smaller intake of nutrients by the grazing cattle, and not to an increase in the energy required for grazing uncut grass. The authors do state, however, that the physical effort of grazing might be high enough, under certain conditions, to deter the cow from consuming to full capacity.

There is little published data showing the relationship between animal behaviour and productivity as measured in terms of liveweight gain, but the results from trials at Cockle Park have indicated a possible relationship between these factors.

In 1949 the behaviour of cattle was studied on three differing swards: (1) a permanent pasture of complex botanical composition; (2) a Cockle Park type ley, and (3) a paddock consisting of both types of herbage.

Nine shorthorn cattle were divided into three groups of similar average liveweight and each group was allocated, at random, to one of the paddocks. The cattle were weighed every fortnight, and their behaviour was observed over a twenty-four hour period, on five occasions during the summer.

In each case the recording commenced early in the day. Hand lamps were necessary during the darkest period of the night. Each animal was recorded separately, and the records were continuous, every activity being noted immediately it was observed.

The following activities were recorded:

Grazing: This included the short periods of time spent in selecting the herbage.

Cudding:

Resting: This was recorded when the animals were lying down but not cudding.

Idling: This was the time spent resting, together with the time spent standing but not grazing or cudding.

The relationship between animal behaviour records and productivity can be illustrated by correlating the various activities with the rate of liveweight gain. It is difficult, however, to interpret the relationship between these two factors since increases in liveweight cannot be measured accurately in a short-term experiment, and grazing records on any one day may not represent normal behaviour.

A comparison of all the grazing records and the corresponding liveweight increase data gave a correlation of —·5294 (n=16) which is significant at the ·02 level.

This negative relationship can be explained in two ways:

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1. High grazing times represent a waste of energy which directly affects liveweight gains.

2. High grazing times indicate inefficient grazing, i.e. a low rate of food intake per unit of grazing time. This is caused by:

(*a*) A waste of time in selecting edible herbage while grazing a sward, which is variable in either botanical composition, or the stage of growth of individual groups of plants.

(*b*) A low rate of food intake per bite. This may be governed by sward height, density or dry matter content.

The Old Grass plot was understocked carrying three cattle on four acres, since the productivity of the Old Grass was expected to be less than that of the ley which carried three cattle on three acres. This resulted in the herbage on the Old Grass paddock growing away from the cattle and becoming very variable in nature. Liveweight gains were inferior on this plot and grazing records were longer. This can be attributed to a highly selective type of grazing.

There was no significant result when the cudding data were correlated with either records of grazing or the rate of liveweight increase.

Two of the main factors which control the time spent ruminating are the amount and quality of the food eaten, i.e. its content of dry matter and fibre. It is reasonable to suppose that an increase in either constituent will result in an increase in cudding activity.

Throughout the results, high cudding records were associated, although not significantly, with high liveweight gains ($r = \cdot2340$, $n = 16$) and low grazing times ($r = \cdot3850$, $n = 16$). It is unlikely that the high rate of cudding was due to a high fibre content, since animals eating this type of herbage would not make the best liveweight gains. It is, therefore, more likely to relate to high food intake and this view is supported by the fact that the correlation between cudding and liveweight gain, although not statistically significant, was positive.

The results of these preliminary observations of grazing behaviour suggest that the efficiency of grazing, i.e. the time required to consume an optimum amount of food, may affect the rate of liveweight gain. It is believed that sward conditions, e.g. height, density, fibre and dry matter content, govern this efficiency. In this experiment the nutritional value of the sward was not assessed since the amounts of food eaten by the cattle were not successfully determined. In later experiments the technique for measuring the growth and consumption of grass was modified.

In 1950, a second experiment was carried out. The original paddocks were sub-divided to give three plots, each of one acre. The same animals were used and the plots were rotationally grazed. Any surplus grass was cut and removed. The procedure adopted was identical for both the Old and New Grass paddocks, so that a comparison could be made between them.

The food intake and the growth of grass was measured by the "difference" technique (Boyd, 1949). Twenty metal cages were available for each plot to protect the herbage from the grazing cattle.

Although the average daily liveweight gain was 3·55 lb. on the New Grass, and only 2·94 on the Old Grass, the difference between the two was not statistically significant.

The cattle on the New Grass spent less time grazing and more time cudding than those on the Old Grass; the differences, however, were not statistically significant. There were no significant differences between the amounts of herbage grown or eaten on the two plots.

It has been suggested that, in the 1949 trial, grazing was inefficient due to over-selectivity and that this was indicated by the negative correlation "Grazing X Liveweight Gain". In 1950 this relationship declined from $-\cdot5294$ ($n = 16$), which was significant, to $-\cdot1768$ ($n = 22$), which

Table I. A Comparison of the Data Recorded During 1950 on the Old and New Grass Plots

	Difference between means	S.E. of difference	*n*	Minimum difference for significance
Live wt. gains (lb./day/animal)	0·61	·899	22	1·86
Time grazing in min.	51·1	26·77	22	55·52
Time cudding in min.	33·0	32·12	22	67·69
Herbage grown	11·39	21·98	198	43·06
Herbage eaten	13·34	9·42	198	18·369

Table II. Variance Ratios Calculated from the Data Recorded During 1950

	Plots	Seasons	Interaction plots X seasons	Animals
	$n_1=1$	$n_1=1$	$n_1=1$	$n_1=1$
	$n_2=13$	$n_2=13$	$n_2=13$	$n_2=13$
Live wt. gain	1·44	10·65**	3·67*	1·38
Grazing	19·72**	19·23**	6·23**	9·58**
Cudding	3·21	13·21**	0·3	4·24*

*=significant at ·05
**=significant at ·01

was not. This indicates a decrease in selectivity of grazing in 1950, probably due to the intensification of grazing management.

This increase in the efficiency of grazing may imply that there was a positive relationship between the time spent grazing and the amount of food consumed. If this were so, then the correlation between grazing and cudding may be expected to be positive. This coefficient when calculated was found to be positive, although not statistically significant. However, since the correlation between cudding and liveweight gain was significantly negative, it is probable that the increase in cudding and grazing times was due to some factor other than an increase in food consumption. It is possible that the fibre content of the herbage might govern both relationships, and, that as the herbage becomes more fibrous, it not only requires more cudding but also becomes more difficult to graze. The variation in fibre content, being seasonal, would have a greater effect within plots than between plots. It is interesting to note, from an analysis of the data recorded in 1950, that for liveweight gain and cudding, the seasonal variation was greater than the variation between plots. This is illustrated by Table II.

It has been shown that animal behaviour records may be related to productivity and could be of value in pasture evaluation studies. The problem is complex and, before records of animal behaviour can be used to interpret variations in pasture productivity, measured in terms of liveweight gain or milk production, the individual and combined effects of all the factors causing variation in animal behaviour must be understood.

It was apparent that visual records of grazing were not accurate, since they included the time spent in selecting the herbage to be grazed; this will result in large variations where pastures show a marked difference. The number of bites per minute of grazing time gives a fair indication of selectivity, whilst the total number of bites of grazing gives a more accurate picture of grazing activity. Records of time spent cudding do not give any information about the number of boli produced nor do they indicate the actual number of chews of cudding. These factors may be important measures of behaviour.

It was necessary, therefore, to develop an automatic behaviour recording apparatus which has been described in a previous issue of this *Journal* (Duckworth & Shirlaw, 1955). Using this apparatus, a detailed study of animal behaviour under controlled conditions was carried out to determine fundamental relationships between food consumption and eating behaviour.

In the spring of 1954, the apparatus was used to obtain a continuous record of the jaw movements of four cows over a period of five days, giving data for 20 "cow-days". The cattle were housed in a specially equipped byre at Nafferton, the commercial farm of Durham University.

Freshly cut grass was fed to the cows each day. The grass was obtained from different fields at various stages of growth. The variation in the herbage is illustrated in Table III.

The cows were each fed 90 lb. of wet grass per day in three feeds of 30 lb. each. The three feeds were offered at 8.30 a.m., 12 noon and 5.30 p.m. Feed residues were bulked and weighed daily.

The food offered each day was sampled and analysed for dry matter and fibre content. The weights of wet matter, dry matter and fibre consumed are referred to as the "feed variables."

To determine possible relationships between feed intake and behaviour records, correlation coefficients were calculated. Three aspects of the food consumed were considered, i.e. the weights of wet matter, dry matter and fibre. These data were correlated with the following aspects of

Table III. To Show the Variation in the Herbage During the Five Days

Day no.	Dominant type of herbage	% Dry matter	% Fibre in dry matter
1	Perennial Ryegrass (after rain)	18·862	28·4
2	Perennial Ryegrass	26·912	28·8
3	Cocksfoot (after rain)	17·45	28·7
4	Italian Ryegrass	23·15	23·5
5	Italian Ryegrass (after rain)	16·925	24·9

eating behaviour:

1. The number of jaw movements associated with eating.
2. The number of jaw movements associated with cudding.
3. The number of boli produced during cudding.
4. The time spent eating.
5. The time spent cudding.
6. The number of miscellaneous jaw movements.

In order to determine the single effect of any one aspect of the feed intake, e.g. the total weight of wet matter or fibre consumed, partial correlation coefficients were calculated. For each correlation coefficient there were 20 pairs of readings, and therefore "n"=18. For the partial correlations "n" was reduced by 1 for each of the variables held constant.

The Effect of Variations in Dry Matter and Fibre Contents on the Weight of Wet Grass Consumed

From the data obtained from this trial, it was possible to investigate some of the effects of variations in dry matter and fibre percentages on the feed intake of the cattle. However, the fact that there was a constant weight of wet grass offered limited the maximum amount which could be eaten. Thus only the effect of any factor which tended to reduce appetite below this maximum could be recorded. A correlation between either the fibre precentage of the wet matter, or the dry matter percentage, with the weight of wet matter consumed may be artificially low.

The correlation coefficient between the percentage of dry matter and the weight of wet matter consumed was —·5787, which is significant at the ·01 level. It would appear, therefore, that as the dry matter percentage increased the weight of wet matter consumed decreased. This is in agreement with the accepted theory that the weight of dry matter consumed is the factor limiting the animal's appetite.

When this correlation coefficient is corrected for variation in the percentage of fibre, however, it is reduced to —·1266 which is not significant. It is possible that fibre content has a more important effect than dry matter percentage and that the close correlation between dry matter and fibre percentage calculated to be ·8428, is the main factor underlying the apparent negative correlation between dry matter percentage and wet matter consumed.

There was a high negative correlation between fibre percentage and wet matter consumed (—·6234). When this coefficient is corrected for variations in the percentage of dry matter it is reduced to —·3188 which is not significant.

It is clear that high dry matter and fibre percentages tend to restrict the weight of wet matter consumed. Of the two, the fibre percentage has the greater effect since the negative correlation between the percentage of fibre in the diet, and the weight of wet matter consumed is higher than that between the percentage of dry matter and the weight of wet matter consumed. This is emphasised by the fact that when the correlation between the dry matter percentage and the weight of wet matter consumed is corrected for variations in fibre percentage, the effect is greater than that obtained when the correlation between the fibre percentage and the weight of wet matter consumed is corrected for variations in dry matter. The logical conclusion is that fibre intake can be a major factor controlling the animals' appetite.

The fibre percentage of the herbage can affect the amount consumed in two ways:

(*a*) An increase in fibre percentage may be associated with an increase in the amount of fibre consumed, and it is possible that this may control appetite.

(*b*) Herbage with a high fibre content may be unpalatable, resulting in a reduced feed intake.

The Effect of Variations in the Weights of Wet Matter, Dry Matter and Fibre Consumed on the Eating Behaviour of Cattle

The correlation between the number of bites of eating and the weight of wet matter consumed was —·5516, which is significant at the ·02 level. When this is corrected for the effect of variation in the weights of dry matter and fibre consumed, it is reduced to —·4589, which is significant only at the 0·1 level.

As the weight of wet matter consumed increased the number of bites of eating decreased. There are two possible explanations for this:

(*a*) Table III shows that the greatest variation in dry matter content of the herbage was caused by rain before cutting. The cows were fed a weighed quantity of wet matter and it is possible that an increase in the weight of wet matter consumed was mainly due to water lying on the surface of the leaves of the grass, and not to an increase in the weight of grass consumed. In this event, a negative correlation between the weight of wet matter consumed and the number of bites of eating would be expected.

(*b*) The increase in the weight of wet matter consumed may not be entirely due to the effect of surface water, but may be associated with a genuine decrease in the dry matter percentage of the herbage. The negative correlation may indicate that in this case less bites and possibly less energy are required to eat a given weight of grass. Under these circumstances, there would be a positive correlation between the number of bites of eating and the dry matter percentage. When calculated this correlation was found to be only ·0532. This indicates that variation in the amount of surface water on the herbage caused the correlation between the number of bites of eating and the weight of wet matter consumed, to be negative.

The number of bites of eating were not significantly correlated with either the weight of dry matter or fibre consumed, although in the latter case the coefficients were sufficiently high to suggest a possible relationship, indicating that food with a higher fibre content may require more chewing before swallowing. Very short grass with a low fibre content, may be swallowed without any chewing at all.

The correlation between the time spent eating and the number of bites of eating was ·4563, which is significant at the ·05 level. This indicates that:

(*a*) The results obtained when the time spent eating are correlated with the feed variables will be similar to those obtained when the number of bites of eating are correlated with the same feed variables.

The similarity between the coefficients is shown in Table IV.

(*b*) The correlation, although significant, shows that some variation in the speed of eating did occur, otherwise this coefficient would have been unity.

The correlation coefficient between the time spent eating and the weight of wet matter consumed was —·6166, which is higher than that between the number of bites of eating and the weight of wet matter consumed. As the weight of wet matter eaten increased, the number of bites of eating decreased, but not to such a great extent as did the time spent eating; the cows therefore, must have eaten the greater weight of wet matter at a faster rate of jaw movement, indicating a positive relationship between the weight of wet matter consumed and the speed of eating, expressed as bites per minute. This correlation was calculated and the resulting coefficient was positive but not significant (·3924). The highest speed of eating was also associated with low dry matter and low fibre percentages in the herbage. This type of herbage is highly palatable and palatability may be positively correlated with the speed of eating.

It has already been suggested that herbage with a high fibre content is unpalatable. In this experiment fibre and dry matter percentages were positively correlated. This could give the impression that herbage with a high dry matter content is unpalatable. Herbage with a high dry

Table IV. A Comparison of the Correlation Coefficients Between the Feed Variables and Bites of Eating and Time Eating

	Wet matter consumed	Dry matter consumed	Fibre consumed
Bites of eating	—·5516*	·0117	·3307
Time eating	—·6166**	·0029	·2244

*Significant at ·02
**Significant at ·01

Table V. The Relationship Between the Number of Chews Cudding and the "Feed Variables".

	"r"	Level of significance
Chews cudding × fibre consumed (wet and dry matter consumed held constant)	·5309	·05
Chews cudding × dry matter consumed (fibre and wet matter held constant)	—·2140	Nil
Chews cudding × wet matter consumed (fibre and dry matter held constant)	·2794	Nil

matter and low fibre content could be palatable and consumed in maximum quantities.

It is also possible that the cows ate fastest on the low dry matter, low fibre herbage because their appetites were not being fully satisfied, it being logical to suppose that an animal will eat at a greater speed when it is hungry, than when its appetite is partially satisfied.

There was also a variation in the speed of eating between the cows. On each of the five days Cow I consumed the least amount of herbage and this was associated with a low speed of eating. This suggests that the animal that eats at the slowest rate, eats the least amount of grass.

The Effect of Variations in the Weight of Wet Matter, Dry Matter and Fibre Consumed on the Cudding Behaviour of Cattle

Three aspects of the cudding behaviour of the cattle were recorded during this trial:

(*a*) The number of chews of cudding.
(*b*) The number of boli produced during cudding.
(*c*) The time spent cudding.

The total number of chews of cudding were not significantly correlated with either the weight of wet matter or the weight of dry matter consumed. The correlation between the number of chews cudding and the weight of fibre consumed was significant. These correlations are given in Table V. It appears that the factor governing the number of chews of cudding is the weight of fibre which the animals consume.

An increase in the number of chews of cudding can be associated with an increase either in the number of chews per bolus, or in the number of boli produced. There was no significant correlation between the number of chews per bolus and either the weight of fibre consumed or the fibre percentage of the diet. On the other hand that between the total number of chews cudding and the number of boli produced was ·6145, which is significant at the ·01 level. An increase in the number of chews of cudding was therefore associated with an increase in the number of boli produced.

Under these circumstances a positive relationship would be expected between the number of boli produced and the weight of fibre consumed. Examination of Table VI shows that although the total correlations between the number of boli and the weight of fibre consumed and between the number of boli and the weight of dry matter consumed are significant (at the ·05 and ·1 level respectively), the second order partial correlations are not.

These results suggest that the number of boli produced are significantly increased by the

Table VI. Correlations Between the Number of Boli Produced and the "Feed Variables"

	"r"	Level of significance
Number of boli × wet matter consumed	—·1837	Nil
Number of boli × dry matter consumed	·4409	0·1
Number of boli × fibre consumed	·4468	0·05
Number of boli × wet matter consumed (fibre and dry matter consumed held constant)	—·1276	Nil
Number of boli × dry matter consumed (wet matter and fibre consumed held constant)	·2133	Nil
Number of boli × fibre consumed (wet and dry matter consumed held constant) ..	·2681	Nil

combined effect of an increase in the weight of fibre and dry matter consumed, although neither fibre nor dry matter have a significant effect by themselves. The fact that the correlation between fibre and boli was higher than that between dry matter and boli might indicate that fibre had the greater effect.

These results indicate that the number of boli produced is dependent on the weight of the more fibrous material in the diet. Finely ground food may not be cudded at all, whereas very fibrous material may be regurgitated more than once for subsequent chewing.

On a uniformly fibrous diet the number of boli produced might be related to the amount of food consumed. On a diet of grass, however, it would be difficult to utilise this relationship, since grass is a very variable material.

The correlation between the time spent cudding and the total number of chews of cudding was ·5308 which is significant at the ·02 level; that between the time spent cudding and the number of boli produced was ·8781, which is significant at the ·001 level. These results show that the time spent cudding is more closely associated with the number of boli produced than with the number of chews cudding.

The only "feed variable" significantly correlated with the time spent cudding was the weight of fibre consumed ($r = ·444$, significant at the ·05 level). This correlation is no longer significant when corrected for variations in the weights of wet and dry matter consumed.

The Relative Merits of Time Studies and Records of Jaw Movements

The correlation coefficient between the number of bites of eating and the time spent eating was significant at the ·05 level indicating a relatively constant speed of eating. In this trial little advantage has been gained by recording the individual bites of eating. Hancock (1954) has shown that with the grazing animal, the intensity of eating varies considerably. Under these conditions records of jaw movements are of greater value than time studies.

No significant second order partial correlation was obtained, when the time spent cudding was related to any of the feed variables. The total number of chews of cudding, however, was significantly related to the weight of fibre consumed, and it has been suggested that the number of boli produced was associated with the weights of both dry matter and fibre consumed. It can be concluded that the more detailed information obtained by the use of a recording apparatus is of greater value than that obtained from time studies alone. If time records can be utilised in animal behaviour studies, they will be obtained more accurately by using an automatic recorder, rather than relays of observers.

Summary and Conclusions

The results of two field trials carried out at Cockle Park Research Station during 1949 and 1950 have been described. Behaviour records on different types of sward were compared and related where possible to liveweight gains. From these results it was concluded that animal behaviour records might be of use in pasture evaluation studies, but that more basic knowledge of the subject was required.

An automatic recording apparatus was developed so that experiments of a more fundamental nature could be undertaken. The apparatus has been described in a previous issue of this Journal. It has been used with cattle, housed indoors, to investigate fundamental relationships between the jaw movements of cattle and the intake of wet matter, dry matter and fibre. The results of this experiment can be briefly summarised.

1. It appears that high dry matter and fibre percentages restricted the weight of wet matter consumed. Of the two, the fibre percentage had the greater effect, and it is concluded that the amount of fibre consumed is a major factor controlling appetite.

2. No significant relationship between the bites of eating and food consumed was recorded. It is probable that this was largely due to the fact that the variation in dry matter and fibre percentages which did occur was caused by surface water (rain) and not to a genuine variation in the nature of the grass itself.

It is important in experiments of this type that cattle are fed to appetite, and are not controlled at a level below maximum intake. Under these circumstances studies of animal behaviour and the factors affecting food intake can be studied together.

3. There was a significant negative relationship between the time spent eating and the amount of wet matter consumed, indicating that the animals ate the greater amount of wet matter at a faster speed.

4. The highest speed of eating was associated with herbage with a low dry matter and fibre content. It is possible that this type of herbage

is palatable and that palatability is associated with speed of eating.

5. It is suggested that herbage with a high dry matter and low fibre content could be palatable and would be consumed in maximum quantities.

6. There was no relationship between the number of chews cudding and the weights of either the wet or dry matter consumed. There was, however, a positive correlation with the amount of fibre consumed.

7. There was no significant relationship between the number of boli produced and the feed variables. The time spent cudding was closely correlated with the number of boli produced, and therefore, as expected, there was no relationship between the time spent in cudding and the feed variables.

It is concluded that before records of jaw movements can be utilised to determine the amount and quality of food consumed, or to indicate the efficiency of grazing, a great deal of fundamental research on cattle housed indoors must be undertaken. Before studies with free grazing cattle can be commenced, it will be necessary to modify the present radio link between the animal and the recorder, to enable several animals to graze together.

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A STUDY OF FACTORS AFFECTING FEED INTAKE AND THE EATING BEHAVIOUR OF CATTLE

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Introduction

The series of experiments into animal behaviour, carried out at King's College, have been designed to investigate possible relationships between the amount and quality of food consumed, and records of eating behaviour. If such a relationship does exist, it may be possible to measure the feed intake of grazing animals, and indirectly, the potential productivity of swards.

From a literature review, it is evident that the factors which govern an animal's appetite are not fully understood. The terms appetite, food capacity and palatability, must be clearly defined. The single and combined affects of the factors affecting food consumption and eating behaviour must be determined.

For greater accuracy in these fundamental experiments, the cattle have been housed indoors, under controlled feeding conditions.

Two treatments are considered in this paper:

1. Variation in the physical form of the diet obtained by chopping silage.

2. Variation in dry matter content of the diet.

Four in-calf Ayrshire heifers were housed in the experimental byre, which had previously been wired for the recorder. For the first seven days of the trial Cows I and II were fed unchopped silage, and Cows III and IV received chopped silage. During the next seven days the treatments were reversed. The cows were fed three times per day, at 8.0 a.m., 1.0 p.m. and 6.0 p.m. In each case the cattle were offered as much silage as they could eat. The feed intakes were measured, and the jaw movements recorded for the last five days of each period.

The silage was variable in quality and tended to be butyric in parts. Samples were taken from each feed and their dry matter content estimated. An analysis of variance was carried out for each recorded factor and this, in some instances, was followed by a covariance analysis to determine:

(*a*) To what extent a variation shown in one factor was due to a variation in another.

(*b*) The significance of the line of regression.

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1. The Effect of Chopping on the Silage Intake of Cattle

The average daily intake of wet matter was 49·3 lb. when the cows were fed unchopped silage. The intake of chopped silage was 45·6 lb. This difference is significant at the ·01 level (variance ratio=8·7, F=7·44). The chopped silage had a slightly higher average dry matter content (0·4 per cent.). It is generally accepted that cattle eat to a constant dry matter intake, and an increase in dry matter percentage would therefore cause a reduction in the weight of wet matter consumed.

When the effect of variations in dry matter percentage were removed by covariance analysis, it was found that there was still a significantly greater weight of unchopped silage consumed, (variance ratio 7·83, F=7·44 at the ·01 level). This result could be expected since the variation in dry matter percentage between the two diets was slight.

The variation in dry matter percentage within treatments, chopped and unchopped, was considerable, (18—24 per cent.), but the line of regression between dry matter percentage and wet matter consumed was not significant, indicating that the cattle did not eat to a constant dry matter intake. It is probable that, for the cattle on both treatments, the weight of wet matter consumed was limiting appetite; and the effect of chopping was to prevent the cows eating to the maximum possible intake for this particular diet.

If the dry matter percentage had been constant for both diets, the lower wet matter intake of chopped silage would have been associated with a lower dry matter intake. When the dry matter intakes were corrected for variatians in dry matter percentage, the difference was significant, (variance ratio=7·15, F=4·14 at the ·05 level of probability). The line of regression between dry matter percentage and dry matter consumed is highly significant, (variance ratio 16·46, F=13·29 at the ·001 level of probability), emphasising the fact that in this experiment the amount of wet silage consumed controlled appetite, and consequently an increased dry matter percentage

Table I. A Comparison of the Eating Behaviour of Cattle Consuming Chopped and Unchopped Silage

	Unchopped average/day	Chopped average/day	Level of sig. of difference
Bites of eating	15,410	17,600	·01
Time spent eating	200 min.	185 min.	·01
Rate of eating (bites/minute)	79·6	83·8	·01

resulted in an increased dry matter intake. The physical form of the diet is an additional factor affecting feed intake.

The Effect of Chopping Silage on the Number of Bites of Eating, the Time Spent Eating and the Rate of Eating

Table I shows that the cows took significantly more bites to eat the chopped silage although the time spent eating was significantly less. A significantly greater rate of eating, expressed as bites per minute, would therefore be expected on the chopped silage.

The number of bites of eating as measured by the recorder consists of two parts which are indistinguishable on the record:

(*a*) A number of jaw movements required to get the feed into the mouth. Observation has shown that these are very rapid.

(*b*) For each mouthful there are a number of slower jaw movements which represent a certain amount of chewing before swallowing.

The greater number of bites of eating when the cows were receiving chopped silage, even though they ate less, is probably due to a decrease in the amount consumed per bite, and to an increase in the number of jaw movements required to get the feed into the mouth, the longer silage being more easily collected. This may be associated with a change in the number of chews before swallowing, the chopped silage requiring comparatively few. If the increase in the first fraction was proportionately greater than the decrease in the second, a greater number of bites, at a faster rate, would have been recorded.

It is interesting to note that the cattle eating a smaller weight of the chopped diet took a greater number of bites. It is possible that the smaller intake of chopped silage might be the result of a fatigue factor, limiting feed intake below the maximum physical capacity of the animal.

In order to investigate the variation in the rates of eating, the number of bites of eating were counted for the first five minutes, the middle five minutes and the last five minutes of each feed for each cow. These were then expressed as bites per minute—Rate A, B & C.

An analysis of variance shows that the difference between the rates of eating is highly significant. The average rate of eating during the first five minutes was 88·0 bites per minute, which is the same as that for the middle five minutes. That for the last five minutes, however, was only 69·0, indicating a rapid fall off in the rate of eating during the last half of the feeding period.

At the beginning of the feeding period the cows tended to eat continuously. Towards the end of the feed, however, gaps of from five to fifteen seconds appeared in the record, during which time the cows stopped eating. The rapid fall off in the rate of eating was due, in part, to the appearance of these gaps in the record with increasing frequency.

The difference between feeds is not significant, and the cows ate each of the three feeds at the same rate, even though the long period before the first feed in the morning may have resulted in the cows being most hungry at this time.

There was a significant difference in the rates of eating between the cows.

The Effect of Chopping Silage on the Cudding Behaviour of Cattle

Table II shows that the cows receiving the chopped silage took more chews while cudding than those receiving the unchopped, and that the difference is significant at the ·05 level. The analysis of covariance, correcting for variations in dry matter intake, reduces the variance ratio from 4·14 to 3·96, which, although very slight, renders the difference between the means insignificant at the ·05 level.

There was a significantly greater number of boli produced on the unchopped diet. This may be the result of the increased weight of silage consumed. When the effect of variations in dry matter intake are removed by covariance analysis

Table II. A Comparison of the Cudding Behaviour of Cattle Consuming Chopped and Unchopped Silage

	Unchopped average/day	Chopped average/day	Level of sig. of difference
Total chews cudding	29,120	31,040	·05
Boli produced	663	616	·05
Time spent cudding	533 min.	515 min.	None

the variance ratio is reduced from 4·37 to 3·25, which is not significant. Chopping the silage has, therefore, not directly affected cudding behaviour. The apparent increase in cudding activity is associated with an increase in the amount of food consumed.

There was no significant difference in the time spent cudding. The variance ratio for the line of regression between the time spent cudding and the number of boli produced is 28·37 (significant at the ·001 level), that between the time spent cudding and the total chews cudding is 7·75 which is significant at the ·01 level of probability. It may, therefore, be concluded that the time spent cudding is controlled partly by the number of chews cudding, and partly by the number of boli produced, the association with the latter being the closer. This relationship has been found in previous experiments.

Discussion

The effect of chopping silage has been:

(*a*) A reduction in the amount consumed.

(*b*) A reduction in the amount of dry matter consumed. This was masked, to some extent, by an increase in the dry matter percentage of the chopped silage.

(*c*) An increase in the number of bites of eating, and the speed of eating, with a reduction in the time spent eating.

(*d*) An increase in the number of chews cudding, and boli produced.

It is interesting to find that, on both diets, the cattle ate to a constant wet matter intake. This emphasises the importance of providing roughage feeds high in dry matter, if maximum utilisation is to be achieved.

Forage harvesters which lacerate crops before ensiling, are valuable for the following reasons:

(*a*) They enable additives such as sodium metabisulphite to spread evenly throughout the silo.

(*b*) Coarse stemmy crops are more easily consolidated.

(*c*) The crop is more easily handled on the silo.

(*d*) The resulting silage may be of better quality. (Murdoch, et al, 1955; Balch, et al, 1951).

(*e*) Chopped material is more easily "grazed" by self-fed cattle.

It is apparent, from the experiment described, that chopping silage does not increase feed intake or reduce the energy requirements of eating.

II. The Effect of Variation in the Dry Matter Content of Grass

Small variations of dry matter percentage in a diet have been shown to have some effect on the feed intake and various aspects of jaw movements in cattle. (Duckworth & Shirlaw, 1958). The full effect of dry matter content was, however, masked to some extent, by the fact that the variations in dry matter percentage were relatively small and due in part, to surface water from rain. In order to bring out more clearly the effect of dry matter percentage, and to make any variation in dry matter percentage within each treatment relatively small, a second experiment was carried out in which fresh grass, and grass artificially dried to twice its original dry matter content, were compared.

The experimental design was identical to that adopted in the previous experiment, the same four Ayrshire heifers being used. Grass was cut fresh each day, half a load being dried for about thirty minutes on a grass drier. Two cows received the fresh grass, and the other two received the dried grass, both pairs being fed three times per day; the cows were fed to appetite.

The method of statistical analysis was the same as that previously used, and the same data were recorded.

The Effect of a Variation in Dry Matter Percentage on the Amount of Grass Consumed and the Quantity of Water Drunk by Cattle

Dodsworth & Campbell (1953) obtained results with sheep, which indicated that as the dry matter percentage fell, so did the dry matter intake, suggesting that in this case the weight of

wet matter consumed limited appetite. In their experiment the variation in dry matter percentages was from 16·8 to 22·6 and was achieved by wetting silage.

Results obtained while studying animal behaviour have shown a high negative correlation between the dry matter percentage and the weight of wet matter consumed, suggesting that the weight of dry matter consumed is the limiting factor in the animals' appetite.

The conclusions drawn from these two experiments indicate that the factors which affect an animal's appetite are not fully understood. It was thought that further information was required to determine more critically, the effect of variations in the dry matter percentage of a diet, on the amount consumed.

In this experiment wet grass, which had an average dry matter content of 24·7 per cent., was partially dried to give an average of 50·9 per cent.

The weights of grass consumed, the weights of dry matter consumed and the weights of water drunk together with the total water intake of the four heifers for each day, were recorded. The total water intake was calculated as follows:

Total water intake=

$$\frac{\text{Weight of grass consumed} \times \text{percentage water content}}{100} + \text{Weight of water drunk}$$

differences in the dry matter percentages between the two treatments, examination of the individual feed intakes of the cows on each treatment, suggested that on the fresh-grass diet, the higher the dry matter percentage, the higher the dry matter intake, indicating that wet matter consumption was controlling appetite.

To investigate this point correlation coefficients between dry matter percentage and weights of dry matter consumed, and between dry matter percentage and weights of wet matter consumed, were calculated from:

(*a*) All the results,

(*b*) the results from the cows when fed partially dried grass, and

(*c*) the results from the cows when fed the fresh grass.

These correlation coefficients are given in Table IV.

The two correlation coefficients calculated from all the results agree with the analysis of variance (Table III), supporting the theory that the weight of wet matter consumed was limited by the dry matter intake, and, hence, negatively related in an almost linear fashion to the dry matter percentage.

Table III. Average Food and Total Water Consumption on the High and Low Dry Matter Diets

	Dried grass average/day	Fresh grass average/day	Level of sig. of the difference from analysis of variance
Weight of grass eaten	35·2 lb.	71·5 lb.	·01
Dry matter percentage	51·0	24·7	·01
Dry matter consumed	17·8 lb.	17·8 lb.	None
Weight of water drunk	53·0 lb.	18·2 lb.	·01
Total water intake	70·4 lb.	72·2 lb.	None

Table III shows a highly significant difference between the amounts of grass consumed on the high and low dry matter diets. The average intake of dry matter, however, was the same whichever diet the cows were receiving. These results suggest that the cows ate to a constant dry matter intake. If this were so, it would be expected that the higher the dry matter percentage, the lower would be the weight of grass consumed. Although this is true with the large

Variations in dry matter percentage on the diet of approximately 50 per cent. dry matter did not significantly affect the amounts of either wet or dry matter consumed.

On the fresh grass diet, the correlation coefficients indicate that the wet matter intake was controlling appetite (dry matter percentage x dry matter consumed = ·8553).

The appetite of the cattle consuming the dry food was controlled by dry matter intake, where-

Table IV. Correlation Coefficients Between the D.M. Percentages and the Amounts of Food Consumed on the Different Diets

The correlation between	Correlation coefficient	Level of sig.
Calculated from all the data (n=38)		
Dry matter % and dry matter consumed	·1376	None
Dry matter % and wet matter consumed	—·9377	·001
Calculated from the data when feeding partially dried grass (n=18)		
Dry matter % and dry matter consumed	·1694	None
Dry matter % and wet matter consumed	—·3960	·1
Calculated from the data when feeding fresh grass (n=18)		
Dry matter % and dry matter consumed	·8553	·001
Dry matter % and wet matter consumed	—·0516	None

as the appetite of cattle consuming the wet diet was controlled by the weight of wet matter consumed. Under these circumstances the cattle on the wet diet should have had a lower dry matter intake. In both cases, however, the average daily consumption of dry matter was exactly the same.

On the wet diets the range in dry matter content was from 19-29 per cent. From an examination of the daily intake figures of individual cows, it is seen that when the dry matter percentage fell towards 19, intake was reduced. When the dry matter percentage rose sharply to 28, the daily intake of dry matter rose to a maximum of 23·9 lb. per day, which was 0·9 lb. higher than the highest dry matter intake on the high dry matter diet (50 per cent).

The relationship between dry matter percentage and dry matter intake, on any one day, appears to be dependent on gut fill, i.e. is affected by the previous day's consumption.

This explains why a common dry matter intake could be recorded, and suggests that a critical level of dry matter percentage, below which the animal is unable to satisfy its dry matter requirement, lies between 19 and 29. A more detailed examination of the records of individual feed intakes, indicates that this range in dry matter percentage can be restricted to 24 to 28, under the conditions of this experiment.

It is apparent, that to get maximum dry matter intake, there is no need to feed a diet higher than 28 per cent. dry matter.

It is well known that, with grassland herbage, dry matter percentage and fibre percentage are closely correlated, and it is possible that on both diets the common dry matter appetite of the cows, recorded as 17·8 lb. per day, could be affected by the level of fibre intake.

Table III shows that, on average, the cows drank nearly three times the weight of water when receiving the partially dried grass, than when receiving the fresh grass. This difference is highly significant. In order to determine whether or not this increase in the weight of water drunk compensated for the difference in the water content of the two diets, an analysis of variance was carried out on the total water intake calculated as above. The difference in total water intake was slight, and the analysis of variance shows that it is not significant. This may suggest that the animal requires a definite quantity of water, the greater part of which can be obtained from fresh grass, but when the grass is dried it needs to drink about the same weight of water as has been removed during the drying process.

The Effect of a Variation in the Dry Matter Percentage of Grass on the Eating Behaviour of Cattle

The number of bites of eating was significantly greater when the cows were receiving wet grass than when the cows were receiving partially dried grass. Since the weight of dry matter consumed was the same on each treatment, it may be concluded that the animals took more bites, when eating wet grass, to eat the same weight of dry matter.

An analysis of covariance, correcting the number of bites of eating for variation in the weight of grass consumed, changes the variance ratio from 27·5 to —63·32. Thus, had the cows

Table V. A Comparison of Eating Behaviour on the Wet and Dry Diets

	Wet grass average/day	Dried grass average/day	Level of sig. of difference
Bites of eating	23,830	19,610	·001
Time spent eating	294 min.	257 min.	·001
Rate of eating (bites/minute)	83·2	80·0	·001

eaten the same weight of grass, the difference between the two treatments would have been even more significant, but would have been reversed; i.e. the cows would have taken more bites to eat the partially dried grass. The explanation for this is that although the cows ate more than twice the weight of wet grass on the fresh grass diet, the increase in the number of bites, although highly significant, was only about one fifth.

In order to eat the same weight of dry matter, cows on the wet diet had to consume a greater weight of wet food, and for this reason, cows on the wet grass took more bites per unit of dry matter intake. This indicates a slight positive relationship between "bulkiness" and low dry matter percentage.

The analysis of variance for the time spent eating shows, that a significantly greater time was spent eating the wet grass than the partially dried grass. This was due to the increased number of bites of eating, as shown by an analysis of covariance between the time spent eating and the number of bites of eating, which gave a regression line significant at the ·001 level of probability.

As in the previous trial, an analysis of the rates of eating was carried out. The rates of eating were shown to be significantly greater when the cows were receiving the wet grass.

Consideration of the rates of eating at the beginning (A), middle (B) and end (C) of the feeds, shows a significant difference between them. This difference has been broken down into its component parts (Table VI), i.e. the difference between rate C and A + B together, and that between rate A and B.

Rate B (82·7 bites per minute) is significantly less than rate A (84·75 bites per minute) at the ·01 level of probability; the difference between rate C (77·4 bites per minute) and rate A and B, is significant at the ·001 level. There is, therefore, a gradual decrease in the rate of eating during the first half of the feed, with a much greater decrease towards the end. Examination of the records has indicated that, although the decrease in the rate of eating during the first half of the feeding period is an actual decrease in the number of bites per minute, that during the second half of the feeding period is due, in part, to a decrease in the intensity of feeding, gaps of from five to ten seconds appearing in the record as in the silage trial. The decrease in the rate of eating during the first half of the feeding period was not seen in the previous trial.

There is a significant difference between the rates of eating of the four cows, but no significant difference between the rate of eating for the three feeds on any one day.

The Effect of a Variation in the Dry Matter Content of Grass on the Cudding Behaviour of Cattle

Table VII shows that although the wet grass diet gave higher records in each of the three aspects of cudding behaviour, in no case were the differences between the treatments significant.

A covariance analysis, correcting for variations in dry matter intake, was carried out in each case. Table VIII compares the variance

Table VI. A Comparison of the Speeds of Eating at the Beginning, Middle and End of Each Feed

	S.S.	D of F.	Variance	Variance ratio
C v. A + B	3242·7	1	3242·7	197·16
Between A & B	252·2	1	252·2	7·93
Error	14344·2	350	41	

For significance at the ·01 level of probability a variance ratio greater than 6·64 is required; at the ·001 level a variance ratio greater than 10·83 is required.

Table VII. A Comparison of the Cudding Behaviour of Cattle on the Wet and Dry Diets

	Wet grass average/day	Dried grass average/day	Level of sig. of difference
Total chews cudding	29,600	28,580	None
Boli produced	572	558	None
Time spent cudding	533 min.	519 min.	None

Table VIII. The Variance Ratios from the Analysis of Variance and Covariance of the Cudding Data

	F calculated from analysis of variance	F calculated from analysis of covariance	F for the line of regression
Total chews cudding	1·4	1·35	0·65
Boli produced	0·75	0·82	2·87
Time spent cudding	0·9	0·87	0·002

ratio between the treatments obtained from the analysis of variance with that obtained from the analysis of covariance, and also gives the variance ratio for the line of regression.

In no case does a significant variance ratio result, and it may be concluded that drying the grass has produced no variation in cudding behaviour, nor can the various aspects of cudding behaviour be associated with the weight of dry matter consumed. This is probably due to the fact that the difference in the dry matter intake was negligible.

Discussion

In the chopped silage experiment, the weight of wet matter consumed controlled appetite. The dry matter percentages of the diets were 20·7 and 21·3. Dodsworth & Campbell (1953), feeding silages of less than 23·1 per cent. dry matter to both cattle and sheep, have also reported that the amount of wet matter consumed can control appetite. Results obtained while studying animal behaviour have shown that where the dry matter percentage rises to 26, the weight of dry matter consumed becomes the limiting factor.

In the present experiment, it appeared that on both the wet and dry diets, dry matter consumption was limiting appetite, since cattle on both diets had the same average, daily, dry matter intake. Close examination of the daily records of the cattle receiving the wet diet, where the dry matter content ranged from 19-29 per cent. showed that when the dry matter content was very low, wet matter consumption controlled appetite. When the dry matter content rose towards 29 per cent. dry matter consumption controlled appetite. There would, therefore, appear to be a critical dry matter percentage, which will determine the factor controlling appetite. Under these particular experimental conditions the critical dry matter percentage was between 24 and 28. No further increase in dry matter intake would be obtained by increasing dry matter percentage above 28.

It is possible, however, that in this experiment some other factor, for example the weight of fibre consumed, could be controlling appetite; if this were so, a diet low in fibre and higher than 28 per cent. dry matter, might have given a higher dry matter intake.

It has been suggested that the fibre percentage of the diet can affect palatability, the weight of fibre consumed and the amount of time and energy spent in cudding. Detailed experiments must be carried out to determine the precise effects of variations in fibre percentage on the appetites of cattle.

On the dry diet, cows drank three times more liquid water than cows consuming the wet grass. The total water intake of the cattle on both the diets was very similar. It would appear therefore that the cattle require a fairly constant supply of water, the greater part of which can be obtained from a food of low dry matter content. In this experiment, it was found that cattle on the low dry matter diets took more bites to consume the same weight of dry matter, indicating

that the wetter diet was more bulky. It may be important to consider the waste of energy involved in consuming wet diets.

It was found that the speed of eating, which was more rapid on the wetter diets, declined rapidly towards the end of each feed. This may be due to a fatigue factor, or, it may be a result of satiation of appetite. If a fatigue factor does operate, it would emphasise the need for a high dry matter diet.

No significant variation was recorded in cudding behaviour, and there is little doubt that this was related to the similarity in dry matter intake on each treatment.

Summary

Two experiments have been reported in which the physical nature of the diet of four Ayrshire heifers was altered by:

(*a*) Chopping silage.

(*b*) Partially drying fresh grass.

The effects of the treatments on both feed intake and jaw movements have been fully discussed.

It was concluded that, on a herbage diet, maximum dry matter intake could only be obtained, when the dry matter percentage was above a critical figure, and that this figure lay within the range of 24-28 per cent.

On diets below 24 per cent. dry matter, the weight of wet matter consumed controlled appetite.

It was found that the wetter diets were more bulky and required more bites of eating per pound of dry matter consumed.

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SOCIAL INTEGRATION OF THE MOOSE CALF

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In a long range study of behaviour patterns in free-ranging ungulates (Altmann, 1949-1957) the Wyoming moose *Alces alces shirasi* provides an opportunity to witness solitary and social phases of behaviour within one species and their step by step integration.

These behaviour studies were carried out from the Jackson Hole Biological Research Station of the University of Wyoming, under the sponsorship of the New York Zoological Society, and since 1955, from the National Science Foundation. This paper attempts to trace and analyse the social integration of the young moose calf within its background.

The ecology and natural history of the North American moose-calf has been dealt with extensively by Peterson (1955) and by Denniston (1956). Since there are many over-lapping instances of observation in the case of Denniston's paper (1956) in which we agree as to the behaviour, but differ in interpretation, I suggest the reading of Denniston's paper (1956).

The material and data of this study were gathered over a period of three years. The moose observations, from hidden vantage points, were arranged to record the moose population in the particular moose habitats under scrutiny. It was considered of importance to keep, wherever possible, continued observations on such recorded moose in order to get sequences of behaviour events, rather than random momentary notes.

The observations concerned the total cyclic events of the moose year, but in this paper mainly behaviour sequences concerned with the young moose-calf have been incorporated. Identity of the animals was in many cases kept for two to four months, in a few cases for six months, but none could be carried through the winter seasons.

The total number of moose-cow-calf observations was 486, and the duration of each observation varied from 5½ hours to 20 minutes. Notes were taken on the spot, and a 30-power B. and L. spotting scope and 7 x 50 binoculars were used. Stalking was done on foot and on horseback, as needed.

In the Jackson Hole area of Wyoming (altitude 6,500—7,000 feet) most moose calves are dropped in late May and early June. A tentative classification of the approximate periods in the behavioural development of the moose calf is given in Table I. The terminology is adapted from Scott (1956).

The first days of the calf are characterised by poor locomotion, closest contact with the moose-cow and establishment of the nursing routine. The moose-cow frequently has to squat low or lie down so that the calf may be able to reach the udder. The nursing intervals seem to

Table I. Tentative Periods in Social Development of Moose-calf

Age of calf	1-3 days	4-20 days	20-90 days	90 days until weaning	weaning-1¼ yr. old
Period name	I Neonate	II "Imprinting" or heeling	III Solitary training	IV Begin of socialisation	V Juvenile group training
Characteristics, activity, and potential.	Poor locomotion. Contactual and ingestive behaviour is established.	Locomotion improves. Allelomimetic.* patterns begin. "Imprinting" takes place.	Radius of activity widens. Investigative behaviour dom. Dam enforces territorial defence, keeps calf from all social contacts.	Dam's rutting season brings bull into group. Calf meets bull and other moose. Social integration under way, but on selective basis.	Socialisation makes progress. Calf is still with dam until next calf is born, then in fringe area.

*After Scott (1956): *Contagious Behaviour.*

be determined by the moose-calf which exhibits a strong et-epimeletic (calling for care and attention) tendency from the very first day. In response to this the moose-dam keeps within a very small area with the calf for the first few days, often only a dozen square feet.

The second period, from 4-20 days of age brings a notable improvement in locomotion for the moose-calf. Still in closest contact with the dam, the calf develops the "heeling" or "following" pattern. The moose-cow's grazing and browsing is still done in a rather limited area; she moves slowly and in apparent consideration of the calf, avoiding obstacles (rivers, ditches, rocks) as much as possible. If the moose-dam leaves the calf, it will be lying down in a well-screened hiding place.

When an intruder moves close to the hidden moose-calf, it may get up, approach and even follow the stranger (man, horse). This reaction has brought many a ranger and fisherman into difficulties because of the threat and vigorous attack of the returning moose-dam in retrieving her calf.

The similarity of this "heeling" tendency in the moose-calf with the "imprinting" described for geese and mallards by European and U.S. scientists (Lorenz, 1935; Hess, 1955), and mentioned by Denniston (1956), is quite obvious for the moose-calf. It appears to be a related phenomenon, although according to our findings up to now, it is not a clearly defined case of imprinting. It lacks irreversibility and a precisely limited sensitive period which are postulated in Lorenz's basic paper. Further work on this situation is under way and will shed some light on the heeling pattern in the moose-calf and in other big mammals. In the moose-calf, the sensitive period for this reaction is flexible. It can be prolonged in the case of orphans or temporarily abandoned moose-calves, but in normal deve opment reaches its peak in the second period (see Table I).

Occasionally a conflict arises from the simultaneous enactment of two calfhood behaviour patterns: the hiding or dodging pattern versus the the heeling pattern. Normally they are successively arranged but if both are activated they can lead to a weird mixture of stop and go patterns. Similar conflicts in fawns of the red deer, roe-deer and fallow deer have been described by Meyer-Holzapfel (1949).

In the third developmental period the radius of activity widens. Investigative behaviour dominates in the calf, the interest in feeding by nibbling browse and grasses is in its first stages. The ring of "sliding territoriality" around the calf is still upheld by the dam.

While the term territoriality usually applies to an area proper, the sliding territoriality of the moose-cow implies the defense of an area around the calf. In case of drift or migration this area shifts with the cow-calf group.

The defence is mostly affected by gestures indicating threat. Other moose just passing through or accidentally feeding near the calf, will yield to the moose-cow's threats immediately and detour with quick, hurried steps or avoid the area in question. A definite expression of submissive behaviour is exhibited by the passing moose (lowered head and neck, and ears in intermediate position). Intruders of other species—coyotes, man, horse, cattle or deer—are challenged too, and if they do not retreat at once, are beaten or pursued for several hundred yards. In such cases, the moose-calf of 2-3 months of age is showing the same stiff warning gait, ruffled neck hair and chewing mouth reaction as its dam. It even folds the ears back when an intruder approaches it. As soon, however, as the calf faces an intruder alone, without its dam being close, the gestures are different; no threat is manifest, the ears are bent forward and the gait is hesitant and slow. An extreme case of territorial defence has been reported by us (Altmann, 1955), in which a moose-cow battled an intruding horse in a stream. The defence of the territory includes, of course, the defence of the calf proper. A violent but successful struggle by a moose-cow to save her new-born calf from the jaws of a bear is reported by Conley (1956).

As the summer advances the investigative behaviour of the moose-calf leads it at times to visit other moose, quite often moose-bulls. The moose-dam will then retrieve the calf, chasing it back without attacking the other moose. This indicates that the territorial attitude is gradually waning at this stage (prerut).

Sparse vocal communication and solitary play activity of the moose-calf are in contrast to other cervids, for instance the wapiti calf. In the following Table II are shown some points of contrast between the moose and wapiti calf.

Gestures rather than warning sounds are used between moose-cow and moose-calf to initiate the flight reaction which is executed early in the second period (Table I).

The "delayed reaction" characteristic for moose consists of a "freezing" stance and a

Table II. Comparison of Behaviour Patterns in Two Wild Ungulates.

Behaviour	Moose-calf *Alces alces shirasi*	Elk-calf *Cervus canadensis nelsoni*
Ingestive Et-epimeletic	Takes initiative to nurse at intervals. Huddles up to dam to be licked and nosed. Close contact.	Is hidden alone or in "pools." Waits for dam to return to nurse and lick.
Communicative Warning, flight.	Sparse vocal expression. Warning by gait and posture. Flight in unison with dam after delayed reaction.	Bark warning causes calf to drop and hide Cow-elk takes off, leaves calf. Back and forth call as a bond on migration route.
Play	Solo play around dam. Rushing and kicking game. Dam does not participate.	Social play with other calves. Tag and rush game. Water game, squealing and rushing. Yearlings and cows participate at times.
Allelomimetic and antagonistic	Executes warning gait and angry bristling up and chewing like dam at 2 mo. up. At times disregards dam's efforts to keep it from other moose.	At time of herd integration, exhibits all gait and posture signals, vocal communication still limited. No antagonistic behaviour observed in first year.
Integration into social group life.	Limited, at 3-4 mo., at rutting period of dam. Loose integration. Stays with dam.	At 3 weeks, during spring migration with nursery-herd.
After weaning	Stays in closest contact with dam.	Stays with herd but at a distance from dam.
At birth of new calf	Outer fringe of area. Many attempts to to return close are frustrated.	Either stays in fringe of herd or joins roaming bands.

pause before taking action. At times this delay is considerably extended so that it appears as if the moose is not reacting at all. Close scrutiny of such situations reveals that the delay in reaction either serves to select time for a screened, silent withdrawal, or for an unexpected attack. The popular belief that moose do not "pay much attention" is erroneous. Even when eagerly browsing, grazing or standing still, the moose will closely observe the disturbance and select the most suitable moment for slipping away.

The transition of the moose-calf from the early calfhood isolation to the "membership" in moose groups in the fall is characterised by a steadily widening circle of investigative activity. In the relation between moose-dam and calf it is evident that gradually more leeway is given to the movements of the calf. This obviously increases the discipline of leadership effectively. For example, if the now larger calf does not follow the dam upon moving into the timber, the moose-cow will not retrieve it, but moves on and waits quietly in the distance until the scared calf arrives in a hurry, anxiously searching and sniffing the dam's tracks. Such reinforcement will make the calf stay in sight of the dam for quite a time.

With the progress of the season and the beginning of the rutting time, the moose-cow and calf will be joined by a bull. All territorial defences of the moose-cow have disappeared by now.

It is obvious that the encounter of the moose-bull with the calf is of importance for his courtship success. A friendly reaction by the bull will let the calf stay close and with it keep the moose-cow contented. If, in the early stages of the rut, for example, the bull intimidates or butts the moose-calf, the cow will not stay but leaves with her calf at once.

Often the calf shows a pronounced interest in the moose-bull—approaches, circles and licks the bulls' flanks with apparent signs of excitement, its hair standing up, and using the stiff gait. It will remain near the bull, if possible, even rest in his proximity.

While the moose-calf is thus integrated into the mating group, the yearling, or last year's calf, has to face another difficult period in its life.

The *first crisis* arises when in spring with the arrival of the new calf, the moose-cow suddenly turned hostile and drove the yearling into the fringe area of her "calf territory."

This event is actually not different from the situation of the elk yearling, but it apparently

affects the moose yearling harder because of its more exclusive bond with its dam.

Only rarely does the moose yearling leave the area of its family group. As a rule it will remain in the fringe and attempt an approach to the dam again and again. But a close approach will not be tolerated by the moose-cow until the barriers of territoriality are relaxed at the onset of the rutting season.

The *second crisis* comes for the yearlings of both sexes in the fall. The female yearling moose will be regarded during the rut as a rival female by the moose-cow and will be kept at an even greater distance. The male yearling moose will be tolerated by its dam, but has to be on guard in respect to the moose-bull. Allowed to stay nearby, he may, however, not show interest in the moose-cow nor approach her and at the slightest provocation will be the target for a violent chase by the big moose-bull. In spite of this constant threat the moose yearling is standing by persistently and often gets a chance to outwit the dominant bull. If the big bull, for example, is engaged in a fight or threat by a rival intruder at a distance, the young moose will quickly seize the chance to approach the moose-cow only to be chased away when the old bull returns. In some cases the mature bull will even interrupt a serious battle for a moment in order to chase the yearling away from the cow.

This second displacement of the yearling gradually precipitates the independence of the young moose from the family group. The roaming stage and the attachment as satellite to an older bull takes place.

The sharply delineated social order of the rutting season begins to deteriorate and odd bands of unattached moose join up to form the winter group. The moose-cow and calf will occasionally join them for a brief stay.

The general weaning process is ending by this time, but the bond between moose-cow and calf remains a close one, more so than in the other members of the cervids. It is a known fact that if the dam is killed the moose-calf rarely survives the winter. Guidance and protection are still needed by the moose-calf. The winter group in moose does not take care of an orphan moose-calf. Under such circumstances the moose-calf may revert to the "heeling response" of its earlier days. It may try to follow another moose or even a mammal of another species. Such attempts may have a fatal outcome. A yearling moose, an orphan, carefully raised and in good physical condition, was put into a large wild-life meadow range area populated by a bison herd. It tried at once to join the bison herd and was gored by a bison cow without delay, although there were no obstacles to an escape or avoidance. The strong competition for the available food during the winter puts the orphan moose-calf way down in the rank order. The moose-calf with a dam would otherwise share the ranking of its dam.

There are four phenomena which stand out in the social maturation process of the moose-calf.

1. The strictly solitary upbringing of the calf by its dam, applying a ring of "sliding territoriality" around it for 90 days.

2. The "imprintability" or heeling response of the moose-calf and its possible later return to this condition if in need of attachment through the loss of its dam.

3. The social integration of the moose-calf during the dam's rutting season.

4. The continuation of et-epimeletic and allelomimetic close bonds between moose-calf and dam beyond the nursing and weaning period into the second year.

Summary

In studies of the patterns of social behaviour in free ranging ungulates over a ten-year period, their organisation in respect to space, season, leadership, communication and reaction to disturbances was investigated.

It was found that the moose is rather unique in solitary habits. It was therefore selected to trace transition and development of solitary and social phases in the life cycle of moose.

This paper analyses the stages in the behavioural development of the young moose, *Alces alces shirasi*, and contrasts its process of socialization with the wapiti calf.

The neonate period with very limited locomotion, the "heeling period" up to 20 days of age and the period of solitary training in a "sliding territory" are shown to bring about a very enduring close bond between the moose-calf and its dam. The enforcement of signals between mother and young and the reaction to intruders is described. The exploratory activity of the calf gradually widens and the moose-cow shows tolerance in giving the calf's movement more "leeway."

The first social contact of the moose-calf with other moose takes place during the rutting season of its dam when the territorial defences of the moose-cow completely fade out. It is a

member of the mating group and is accepted by the moose bull.

Later the moose-calf joins the loose winter aggregates along with its dam. An orphaned moose-calf will not be integrated and will rarely survive the winter.

The male yearling near his dam is treated as a rival by the moose bull; the female yearling experiences hostility from its own dam during the rut.

Despite such temporary displacements into fringe areas, the moose yearling continues to be dependent on its dam often for another year, long after the weaning process has ended.

In absence of the dam, the moose yearling in need of attachment reverts frequently to the heeling response of its early stage. This response may have a fatal outcome since such attachments may be in disregard of species compatibility.

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EXTERNALLY-AROUSED DRIVES IN THE RACOON

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A number of studies emphasize the importance of the manipulation-curiosity-exploration type of motive. Early among these are the studies by Harlow, *et al* (1949) where it was demonstrated that monkeys could learn to solve mechanical puzzles on the basis of the manipulation motive. These studies were extended to include discrimination learning with the investigations by Harlow & McClearn (1954) and Butler (1953). These latter investigations were more specifically concerned with visual exploration motivation.

That such externally-elicited drives are not restricted to monkeys is attested to by the studies of Berlyne (1950, 1955), and Montgomery (1951, 1952) with rats, and Welker (1956) with chimpanzees.

The experiments herein reported were designed to augment the data of comparative psychology with respect to motivational processes. The raccoon is a logical animal for an investigation of the externally-elicited drives because these animals, as carnivores, are between rats and monkeys on the morphological scale. Also, the raccoon apparently displays a high degree of curiosity and manipulative behaviour as observed by a number of investigations (Cole, 1907; Davis, 1907; McDougall & McDougall, 1931). Specifically, these studies have been concerned with whether curiosity and manipulation can be used to motivate the learning of a simple position response, and whether satiation effects are present.

Experiment 1

Method

Subjects. The subjects used were two male and one female raccoon all of which were approximately one year of age. These animals had been previously tamed and adapted to the experimental situation.

Apparatus. A single-unit T-maze comprised the basic apparatus. The alleys of the maze were completely enclosed except for a wire screen top. Each alley measured 12″ x 30″ x 16″. Another wire cage 15″ x 26″ x 18″ was used as a starting cage. Wooden guillotine doors were located at the point of entrance into the maze, at the immediate entrance to both arms, and at the end of both arms leading into the goal cages. All doors could be controlled by the experimenter from a central point located at the starting cage.

The incentive condition consisted of a series of common objects each suspended by an individual chain and arranged to hang in front of the goal cage. Thus, an animal could reach through the end of the goal cage farthest from the maze and manipulate any of the objects.

Cardboard shields were used to block the animal's view of the experimenter and the goal cages from the starting box. Uniform illumination of the experimental room was provided, and attempts were made to minimise all possible extra-maze cues.

Procedure. Following the procedure used by Montgomery (1954) four free-choice trials were run without incentive conditions to ascertain turning preference. The animals were run for a total of eight days during the learning series. Five trials per day were run for the first three days, and eight trials per day were run for the remaining five days.

Since no turn preference was manifest on the preliminary test trials, all animals were run with the incentive conditions located at the end of the left goal cage.

A trial consisted of placing the animal in the starting cage and with all guillotine doors up permitting him to proceed toward one of the goal cages. The guillotine doors were lowered, when appropriate, to prevent retracing. The animal remained in the goal cage for one minute. Following this, he was placed in a transport cage and removed from the experimental room while the maze was prepared for the next trial.

The stimuli for all animals consisted of the following objects: a plastic cigarette case, a small roll of paper, a two-inch block of unpainted wood, a ball of aluminium foil, a silver spoon, and a small section of white cotton cloth.

On the day following completion of the learning series, new stimulus objects were placed outside the right goal cage and a reversal series was begun, with a total of 55 trials.

The stimulus objects consisted of a two-inch rubber ball, a small plastic toy, a roll of string, a toy rubber dog, a ball of aluminium foil, and a piece of plaid cotton cloth.

Table I.

Learning Series									
Eleven-trial blocks	% Correct turns			Latency (seconds)			Manipulation time (seconds)		
	Sadie	Chick	Cisco	Sadie	Chick	Cisco	Sadie	Chick	Cisco
1	64	55	62	48·4	12·0	12·0	50·0	7·8	17·0
2	64	73	25	17·0	6·5	10·0	50·0	3·7	21·0
3	73	73	62	8·0	3·1	23·2	57·6	4·6	52·2
4	73	100	13	4·5	11·0	5·0	48·7	16·4	59·0
5	55	100	75	11·0	3·4	2·3	44·8	29·9	40·8
Reversal Series									
Eleven-trial blocks	% Correct turns			Latency (seconds)			Manipulation time (seconds)		
	Sadie	Chick	Cisco	Sadie	Chick	Cisco	Sadie	Chick	Cisco
1	64	0	25	17·0	—*	3·5	59·0	—*	58·5
2	73	27	75	6·9	7·0	2·5	57·3	13·0	55·8
3	64	27	63	3·3	17·3	3·75	58·1	3·0	46·4
4	73	45	50	2·9	12·2	33·2	54·5	21·4	55·0
5	64	18	50	9·1	8·5	10·0	53·1	1·5	50·7

*No data reported as no correct turns were made during this block of trials.

Design. For the learning series, the proportion of turns to the correct side was analysed against the hypothesis of chance expectancy. In analysing the reversal data, the proportion of times each animal had turned to the incorrect side was used as the base against which to evaluate any increase in the number of turns to that side.

Results

In terms of correct responses (Table I), only one animal (Sadie) showed a significant change in performance, during both the learning and the reversal series. Chick, although turning to the correct side a significant number of times during the learning series, failed to show any significant change during the reversal series. Cisco failed to perform above chance in either series. The manipulation time of Sadie reveals no significant decline in either the learning or reversal series. For Chick there was a much lower manipulation time during both phases. Response latency reveals a declining trend during the learning series and shows little change during the reversal series. Cisco's data reveal an increase in manipulation during learning and remain high during reversal. His latency data decline (with the exception of Trial Block 3) during learning but an increase in latency occurred during reversal.

All reported latencies are in terms of time to enter the correct alley.

Experiment 2

Method

Subjects. Five newly weaned raccoons (Cleota, Harry, Dick, Edith, and Karl) served as subjects.

Apparatus. The same equipment was used in this experiment with the addition of some new objects for manipulation.

Procedure. After a test of four trials for turn preference revealed no consistent tendencies the animals were run five trials per day for six days. The procedures for each trial were identical to those used in the previous study, with the exception that time was recorded for the opening of the starting door until entry into the goal cages.

The reversal series was also run five trials per day for six days.

In order to provide information on possible satiation effects, the reversal series was extended for an additional six days of five trials each. This series is designated the satiation series.

Statistical Design. The analysis performed on the turn data was the same as that employed in the preceding study. In addition, for each series, trials were grouped in blocks of ten and a repeated measures, single-classification analysis of variance was performed on mean log latency and on mean log manipulation time. The log transformation was used to normalise the distribution.

Product moment correlation coefficients of log manipulation time with log latency were determined for the learning series, and each correlation was tested for significance from zero.

Results

Four of the five animals (Cleota, Harry, Dick and Karl) showed a significant preference for the

Table II.

	% Correct turns			Latency (sec.)			Manipulation time (sec.)		
	Ten-trial blocks			Ten-trial blocks			Ten-trial blocks		
	1	2	3	1	2	3	1	2	3
Learning Series									
Cleota	60	90	100	58·9	18·6	9·6	6·3	25·2	56·3
Harry	80	80	100	83·2	11·8	8·1	12·5	47·9	55·0
Dick	60	100	60	97·7	31·6	22·9	45·7	24·0	14·5
Karl	80	70	100	77·6	29·5	12·3	11·0	19·1	50·1
Edith	60	50	70	49·7	107·0	45·4	21·8	21·9	5·9
Reversal Series									
Cleota	10	70	60	10·0	6·9	21·9	58·9	55·0	52·2
Harry	50	80	60	15·8	7·9	21·9	57·6	53·7	49·0
Dick	60	40	70	8·3	12·6	7·9	46·8	38·9	10·9
Karl	50	40	60	25·7	12·0	17·0	57·5	41·7	24·6
Edith	80	50	60	20·4	15·1	24·5	9·1	9·8	3·4
Satiation Series									
Cleota	60	80	80	6·6	11·0	15·1	40·9	17·6	10·0
Harry	60	60	90	7·7	7·9	8·2	46·0	52·4	26·0
Dick	50	20	40	10·7	9·5	6·5	9·7	15·2	9·5
Karl	70	30	50	17·4	24·9	17·5	7·3	3·1	2·8
Edith	80	50	50	13·5	9·8	12·7	1·9	1·9	2·8

correct side during both learning and reversal series (Table II). The fifth animal (Edith)) failed to demonstrate significant preference during either series.

Mean latency and manipulation time are also presented in Table II. For all animals (with the possible exception of Edith) there was a marked decline in latency during learning which tended to stabilise during the reversal and satiation series. Manipulation time increased steadily in the learning series for three of the five animals (Cleota, Harry and Karl) and gradually declined for all animals during reversal and satiation.

The correlations between log latency and log manipulation for Cleota, Harry, Karl and Dick are —.25, —.57, —.64, and .47 respectively. Those of Harry and Karl differ significantly from zero at the one per cent level.

Analyses of variance were conducted on the learning series data of Cleota, Dick, Harry and Karl and the manipulation data of Cleota, Harry, and Karl. The removal of the data of Edith and Dick is justified by virtue of the fact that the present study was more concerned with uncovering consistencies in behaviour rather than making inferences to raccoons in general. The analyses of latencies revealed significant differences at the .01 level between trials for both the learning series and the reversal series. No differences were found between trials on the satiation series. The analyses performed on the manipulation scores for Cleota, Harry, and Karl showed a significant between trials effect on the learning series and the satiation series.

Discussion

Evidence was obtained in the initial experiment that a manipulatory incentive sufficiently motivated one animal to make a significant number of correct turns in a T-maze situation. Inasmuch as this animal never reached perfect performance for any block of trials it is possible that exploration or curiosity was confounded with manipulation. Consequently one might hypothesize that the manipulatory objects did not provide a strong enough incentive to completely overcome the animal's curiosity of the other arm of the maze.

Due to the small number of subjects employed and the rather pronounced individual differences among the three animals used in the first experiment, further investigation seemed feasible. The possibility that more consistent results might be obtained using younger animals was suggested by the research of Welker (1956). He had found greater curiosity in younger than in older chimpanzees. Also the possibility of sex differences being important was not assessable in the initial study.

The results of the second investigation support those of the first study in showing that a manipulation motive can be sufficient for the learning of a position response. Furthermore, there is evidence to suggest possible age difference in favour of the younger animals. As to the question of a sex difference this study seems to indicate that none is apparent. Of course, it is possible that there is an age-sex interaction which cannot be evaluated by recourse to these data.

It is recognised that these two experiments fall far short of providing definitive data regarding externally-aroused drives. However, they are of significance from the standpoint of providing a base line for further experimentation. Furthermore, they do support the data gathered on other species in indicating the existence of such motivating conditions.

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DISCRIMINATION OF SMALL INTERVALS AND OBJECTS BY RACCOONS*

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Before extensive comparative behavioural data can be obtained from a particular species, the relevant perceptual abilities of that species must be determined (Tinbergen, 1951). Stimulus situations depend on sensory capabilities (Klüver, 1933). Investigation of these capabilities thus logically precedes behavioural experimentation (Watson, 1914).

The following studies were designed to determine the ability of raccoons to perceive visual stimulus materials of the type used in the Wisconsin General Test Apparatus. This apparatus and the associated methods and materials have been standardised and in constant use for two decades or more, since Klüver's demonstration of their value in the study of psychological processes (Klüver, 1933; Lashley, 1938). They afford a means of obtaining data that is characterised by needed continuity of investigation (Peters, 1948) and comparability with existing data from other species (Brogden, 1951; Schneirla, 1952), once perceptual capabilities are known.

The first researches into the vision, as well as the general behaviour of the raccoon, seem to be those published by Cole in 1907, and by Davis, in the same year. They agreed that the animal can discriminate quite capably between small differences in brightness. Cole also reported discrimination between a circle and a square both 6″ in height, and between squares of $6\frac{1}{2}$″ and $4\frac{1}{4}$″. Cole & Long (1909) claimed colour discrimination by their raccoons, although it was difficult for the animals. However, they admitted that their method of brightness control, basically that of producing equivalence for the human eye, might be inadequate for the problem. The subsequent demonstration that brightness equality for humans is not equality for rats (Munn, 1950) indicates that this could well be the case with any other species. Munn (1930) found raccoons responding to brightness when confronted with pattern and brightness differences and concluded that they were incapable of pattern discrimination. Fields (1936) discovered this to be true for small figures of the size Munn had used. Those less than 55 sq. cm. in area were increasingly difficulty for raccoons to discriminate. However, larger figures were discriminated.

Cole (1907) had reported raccoons as nearsighted; they could not discriminate distant objects. Bierens de Haan (1932) decided they were farsighted, and could not distinguish close objects.

These findings, particularly those of Fields, indicate that the problem of vision that would most directly affect the performance of raccoons in a test apparatus of the Wisconsin type is that of acuity. Brightness discrimination has been demonstrated adequate, and recent investigations (Johnson & Michels, 1958) have shown that raccoons are able to discriminate shapes successfully in sizes ranging from one to six inches in maximum linear extent. But ability to discriminate smaller forms and shapes, and perhaps brightness of small areas, is at present questionable.

There are two types of visual discrimination tasks in the Wisconsin tests. The first type, exemplified by patterned string tests, requires the subject to disentangle the stimuli visually in order to obtain a reward which lies beyond his reach. Solution of this type of problem depends upon the ability to distinguish small intervals. The second type of problem requires the subject to distinguish objects, or relationships among objects, in order to secure a reward that is usually within reach. Success here depends upon whether or not the objects themselves are distinguishable, one from another.

The experiments here reported investigated these two aspects of raccoon visual ability in regard to the relevant tasks. They might be thought of as "representative" in design, in Brunswik's sense (Brunswik, 1956), in that stimulus situations were constructed to be samples of usual testing situations rather than to determine isolated psychological limits.

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PLATE I

Fig. 1. Test apparatus in use in an experiment similar to the one herein reported.

Experiment I. Small Interval Discrimination

To undertake the measurement of visual capability from the minimum separable aspect, the method devised by Warden, Fjeld & Koch (1940) was employed. They found, in string tests with monkeys, that widening the space between the strings enabled some monkeys to succeed on problems which they could not otherwise solve. They regarded this interval distance as an index of the perceptual ability of the monkeys in this situation.

Method

Subjects. The subjects for this experiment were three raccoons, *Procyon lotor*, 14 months of age. Chick and Cisco were males; Sadie was female. They had previously been tested on patterned string problems.

Materials. The apparatus used was a replica of the Wisconsin General Test Apparatus. Specifically, this consisted of the following components.

A test-transport cage had interior dimensions of 15″ × 16″ × 24″. The floor was plywood, with sides and top of welded wire mesh over wood framing. The front was open with ¼″ round bars from top to bottom at two inch intervals. The back was formed by a ⅛″ Masonite guillotine door.

Two Masonite screens, 17″ × 27″ were fixed 21″ apart, each with a supporting framework within which they could be raised and lowered. The rear screen contained a half-silvered one-way vision window, 9″ × 6″. The screens were balanced by counterweights, and were operated from the rear screen framing by means of cords and pulleys. A 25-watt bulb was mounted in a reflector overhead midway between the screens.

The whole apparatus was placed on a table, such that the test transport cage could be placed adjoining the forward screen framing, as illustrated in Plate I.

The stimuli were presented on a 16½″ square plywood board, painted neutral gray. Two 14″ chains were fastened at the edge of the board nearest the cage by eyehooks placed 12″ apart. A lucite screen, 3″ high, was mounted on the edge of the board between the cage and the eyehooks. There were 1½″ × 2″ holes in the screen, at the eyehooks, through which the subject could grasp the chains. This served to restrict the responses to correct and incorrect categories.

The reward, a peanut, raisin, or piece of rat diet pellet, was placed in a round black metal cup, 1¾″ in diameter and ½″ deep, which was attached to the free end of one or the other chain in a predetermined Gellerman sequence (1933). To obtain the reward, the subject had to draw in the one chain to which the food cup was attached. In order to choose the correct chain, the subject had to be able to distinguish the interval separating the chains at the point of attachment to the cup. This point was always 14″ from the lucite screen.

Procedure

Trials were conducted in blocks of 12, and the criterion used was 3 or fewer runs* of correct or incorrect responses in a block of 12 trials, with at least 7 of the 12 responses correct (P=·025) (Swed & Eisenhart, 1943).

For the initial block of trials, the chains were placed parallel, 12″ apart, throughout their length. Testing trials were not commenced until the criterion was met at this 12″ distance between chains. For the test trials, the ends of the chains where the food cup was attached, were placed various distances apart. Eight blocks of 12 trials each were presented at each of the following separation distances: 8″, 4″, 2″, 1″ and ½″. Thus each animal performed 96 test trials at each of the separation distances. The sequence of these blocks of trials was randomly assigned. To insure that, insofar as possible, the animal maintained efforts to distinguish the chains, a procedure similar to that used by Lashley (1930) was employed. Whenever the criterion was not met, the next trial block was run at the 12″ interval. Whenever the criterion was met, at either the 12″ or some test interval, the next test trial block from the established random sequence was presented. Thus every block of test trials was preceded by a trial block in which the criterion was achieved.

The animals were run for as many trials per day as they would readily perform. This was ordinarily from 60 to 96 for Cisco, and from 148 to 192 for Sadie and Chick.

Results

The results of the test series indicated that the animals were successfully discriminating the smallest interval (of ½″) between chains. How-

*A run is defined as a succession of identical events which are followed and preceded by different events. For example, a series of correct and incorrect responses occurring in this order + + − − − + − − + + + begins with a run of 2 correct responses, which is followed by a run of three incorrect responses, etc., amounting to five runs in all. The total number of runs indicate whether or not the sample is random. Too many or two few runs in a sample of a given size indicate departure from random distribution with the probabilities presented in the Swed & Eisenhart tables.

aver, there were considerably fewer correct choices when the interval was 2″ or smaller than when it was 4″ or 8″. Therefore, a second series of tests was performed at separation intervals of 3″, ¼″, and 0″, i.e. with the chains touching each other at the point of attachment to the cup. The combined results of both series of tests are presented in Fig. 2. Discrimination deteriorated progressively for intervals smaller

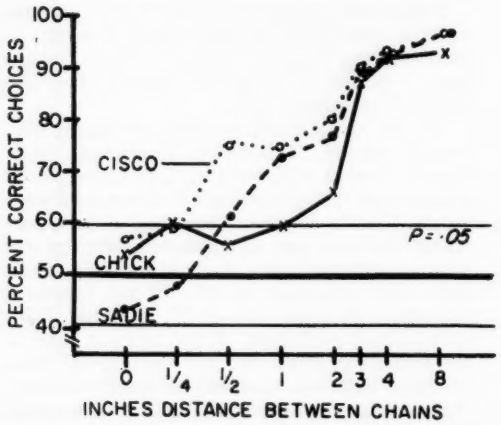

Fig. 2. Interval discrimination by three racoons at a distance of 14 inches—combined results of both test series. Each unit on the horizontal axis represents a doubling of the test interval, except for 0 inches and 3 inches, which were interpolated. In a two choice situation, where 96 choices are made, only ·05 of the means of randomly distributed choices would fall outside the limits designated P=·05.

than 3″, and failed completely when the chains touched each other. However, the animals demonstrated some discrimination at an interval of ¼″. The same results are evident in Fig. 3, which presents, instead of the percentage of correct responses, the number of trial blocks for all animals in which the runs criterion was met.

Experiment II. Discrimination of Small Objects

To measure ability to discriminate small objects, the animals were required to learn to discriminate between two objects approximately one cubic inch in size. After this learned discrimination, they were presented with progressively smaller replicas of the stimulus objects. Consistent correct choice was then considered evidence of discrimination. Variation of maximum linear extent of stimulus objects from one to six inches had produced no effect on discrimination by these subjects in a previous study

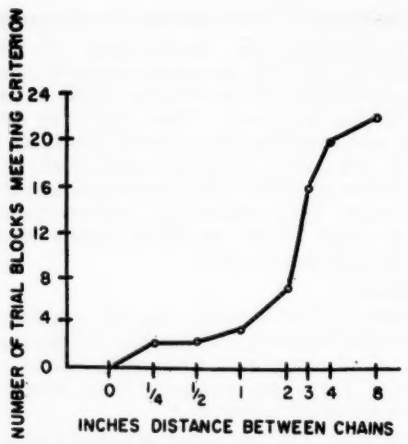

Fig. 3. Interval discrimination by three racoons at a distance of 14 inches as indicated by the number of trial blocks, for all animals, in which the runs criterion was met

(Johnson & Michels, 1958) during which the animals had developed efficient discrimination learning sets.

Method

Subjects. The subjects were nine raccoons, four of whom were 17 months old, the others were 5 months old. Three of the older raccoons were the subjects of the experiment reported just previously. All the subjects had also served as subjects in studies of object discrimination learning sets (Johnson & Michels, 1958) and of manipulative motivation(Thackray & Michels, 1958).

Materials. Using the same apparatus as in the first experiment, the stimuli were here presented on a 1″ × 6″ × 15″ wooden tray, painted neutral grey, in which were two food wells 1″ × ½″ in area and ½″ deep. The food wells were 7″ apart, and were centred 1½″ from the cage edge of the tray. The tray rode on an aluminium cart, which was pushed to the edge of the cage to present the stimuli.

The test materials consisted of three problems, designated A, B, and C.

The objects comprising Problem A were four pairs, each consisting of a polished solid aluminium cube and a cylinder of the same material. The largest pair was a 1″ cube and a cylinder 1″ in diameter and 1″ high. The three other pairs were identical in formation except that the common dimension, instead of 1″, was, respectively, ½″, ¼″, and ⅛″.

The objects in Problem B were pairs each consisting of a polished steel sphere and a four-sided steel pyramid. The sphere of the largest pair was 1″ in diameter; the pyramid had a 1″ square base and was 1″ high. This pair was repeated in $\frac{1}{2}$″, $\frac{1}{4}$″, and $\frac{1}{8}$″ sizes.

Problem C consisted of pairs of identical brass screws. One member of each pair was mounted vertically with the head uppermost. Its mate was also mounted vertically, but with the head concealed in the stimulus base. The largest pair was 1″ Number 6-32 screws, the next smaller was $\frac{1}{2}$″ Number 6-32, the next $\frac{1}{4}$″ Number 2-56 screws, and the smallest $\frac{1}{8}$″ Number 2-56 screws.

All problems were mounted on 2″ × $\frac{3}{8}$″ plywood squares that had been painted flat black. When, as will be seen, these bases proved inadequate, 2″ × 1$\frac{1}{4}$″ black plastic wall tiles were substituted. The objects in Problems A and B were cemented in the centre of their respective tiles; those in Problem C were secured with nuts.

Procedure.

During testing, at least one object of the pair being used was rotated 180° between trials, so that the shape of the stimulus object would be the only cue that was constantly rewarded. That is, the details of the stimulus bases would appear in different relationship from trial to trial, and would not as readily be associated with reward. Since the problem objects were all quadrilaterally symmetrical, the reward was associated with a constant stimulus shape.

For the first trial of a particular problem, raisins were placed in both food wells of the stimulus tray, which were then covered with the 1″ sized pair of stimulus objects. To eliminate object preference factors which might delay learning, whichever object the raccoon selected to displace was thereby designated the correct object, and thenceforth was the only one rewarded. The position of the correct object was randomly determined according to a Gellerman (1933) sequence. Non-correction procedure was followed.

For the subject to learn the discrimination, trials continued with the 1″ objects until a criterion of 9 correct choices in a block of 10 trials was achieved. This somewhat stringent criterion not only required that the animal discriminate, but that he respond consistently and correctly.

When the criterion was met, the $\frac{1}{2}$″ objects were presented for the next 10 trials. Then followed 10 trials with the $\frac{1}{4}$″ objects, and 10 with the $\frac{1}{8}$″ objects. This constituted a preliminary series to familiarise the subjects with all the objects and sizes. The test series commenced with this series repeated in reverse starting with 10 trials at $\frac{1}{8}$″, and concluding with 10 trials at 1″. Another descending series, 10 trials at each size, was followed by a final similar ascending series.

The first 10 trials at each of the sizes were considered influenced by various learning factors, and were not scored. The scored trials began with the second 10 trials at $\frac{1}{8}$″; thus there were 30 scored trials in each size. The score was the number of correct choices of the 30 trials.

The objects were located about 5″ from the animal's eyes at the time of response.

Each animal completed one problem each day for three successive days. The order of problems for each animal was determined so that each problem would appear three times in each sequential position (1st, 2nd, 3rd.).

Results

The first animal to be run, Cisco, on his first problem (Problem A) learned the problem in its 1″ manifestation in 30 trials. On the next series of trials, at the $\frac{1}{2}$″ size, 7 of the 10 responses were correct. Four of 10 choices of $\frac{1}{4}$″ objects were correct. Of the choices of $\frac{1}{8}$″ objects, 10 of 10 were correct. Proceeding upon suspicion, the $\frac{1}{8}$″ stimulus objects were removed from their wooden bases. The bases were then presented over the food wells, and he again chose correctly 10 times in 10 trials. Between each trial the bases were rotated 90° in opposite directions, and the position of the rewarded base was determined by the Gellerman sequence. The only apparent cues for his successful discrimination of the intendedly equivalent bases were the surface textures of the painted wood. At least these were the cues to which the experimenter resorted in order to distinguish them, and for him the discrimination was neither readily nor rapidly accomplished. This argues for a degree of what might be called textural acuity of vision on the part of this animal.

This of course eliminated the wooden bases from the experiment. The plastic tile substituted was free from surface differences. Although it was readily marked with human and raccoon fingerprints which could not be completely removed, their position and pattern could be altered by wiping, as well as by the 180° rotation, between trials.

The scores obtained using the tile bases were analysed for the effects of object size and of

problem order. A preliminary analysis had shown no effect due to difference among the three problems, A, B, and C. The main analysis is summarized in Table I. The effect of problem object size on discrimination is illustrated in Fig. 4.: there was no difference in performance from one size to another.

Table I. Summary of Analysis of Effect of Problem Size and Order

Source	Degrees of freedom	Mean square	F
Between Ss	8	82·17	
Within Ss	(99)		
Size	3	5·54	·84
Order	(2)		
Linear	1	93·39	5·42*
Deviations	1	1·50	
Size x Order	6	5·95	·89
Ss x Size	24	6·46	·96
Ss x Order	16	17·25	2·57**
Ss x Size x Order	48	6·70	
Total	107		

*Significant at ·05 level
**Significant at ·01 level

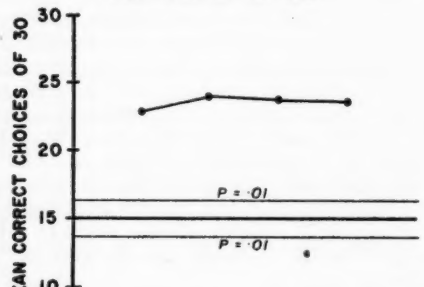

Fig. 4. Discrimination of various sizes of objects by nine raccoons at a minimum distance of 5 inches, as indicated by the mean of the number of correct choices out of a possible 30. In a two-choice situation, where 30 choices are made by 9 animals on each of 3 problems (N=810) only ·01 of the means of randomly distributed choices would fall outside the limits designated P=·01.

All were discriminated with a significant degree of accuracy, indicating that raccoons can distinguish with apparent ease the smallest sizes of stimulus objects that could practicably be used in this type of situation. The effect of problem order is represented in Fig. 5: performance improved from any one problem to succeeding problems,

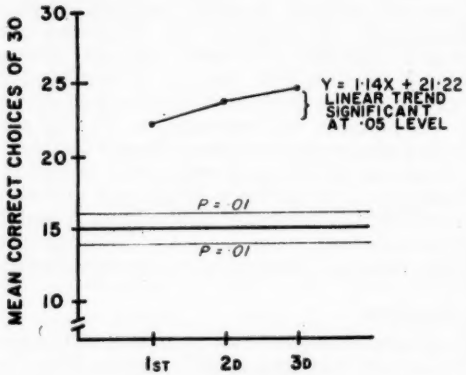

Fig. 5. The effect of experience on discrimination. The mean number of correct choices for all sizes by nine raccoons is presented for problems according to sequential order. In a two-choice situation, when 30 choices are made by 9 animals on each of 4 sizes (N=1080) only ·01 of the means of randomly distributed choices would fall outside the limits designated P=·01.

following a linear function given by the formula: $Y=1{\cdot}14X + 21{\cdot}22$. This departs significantly from the horizontal at the 5 per cent. level, as can be seen in the analysis in Table I. This might be considered as an improvement in discrimination as a result of practice, or as a learning of acuity.

Discussion

Most studies have reported acuity in terms of the minimum visual angle subtended by the discriminanda, whether interval or object. In these terms the raccoons discriminated intervals subtending 61 minutes of arc ($\frac{1}{4}$″ at 14″), and objects subtending 86 minutes of arc ($\frac{1}{8}$″ at 5″). These gross measures cannot be considered as limits of resolving power; they were not intended as such. The purpose of the studies was to determine the functional acuity in a particular situation, that is, what can serve as effective stimulus cues in the Klüver-Wisconsin apparatus.

The larger of the angles obtained, 86 minutes for the $\frac{1}{8}''$ objects, is not a limit of any sort, since there was no decrement in discrimination evident. This indicates that minimal acuity is considerably finer than that needed for this minimal practicable size of three dimensional objects.

However, there was a progressive decrement in interval discrimination for separations smaller than 3″, thus for visual angles smaller than 12 degrees. This may have been due to any of several factors, or combinations of these, which could all be considered as possible limitations upon the visual capacity.

First, in the chain pulling tests, the brightness and contrast differences in the stimulus materials were not optimal for fine visual discrimination. The chains and grey board did not offer the same contrast as did the metallic objects on their black bases. But the chains and board are representative of the materials used in many general behavioural investigations.

Secondly, the relative lack of overlap of the visual fields of the raccoon's eyes may interfere with resolution at any distance. There may be decreasing overlapping of retinal images, with consequent doubling or blurring of impressions. An essential future step in the investigation of raccoon visual ability is the determination of such structural correlates. Apparently the only available information about the ocular anatomy is that noted by Vincent (1912): the central area of the fundus is covered with yellow patches, with a darker periphery; the optic disk is vertically oval; the sensitive area is band-like, 5-7 mm. horizontally across the retina above the nerve entrance; a fovea is present; the pupil is circular; lens fibres are arranged concentrically; both rods and cones are present; and the divergence of optic axes is 25 to 30 degrees, wider than that of dogs (5-25 degrees) and cats (7-9 degrees), narrower than rats (60 degrees) and horses (40 degrees).

Finally, the relative inexperience in visual concentration at that stage of experimentation may have been responsible for the decrement in interval discrimination. There is accumulating evidence that perceptual ability is a function of experience, or learning—in this sense the terms are equivalent. Bevan & Zener (1952) found form perception limens to decrease as a function of practice and experience by human subjects. Recent investigations have demonstrated that stimuli presented to a particular human retinal area became more discriminable through training (Shoaf, 1957), and that visual perceptual judgments improve with practice without knowledge of their correctness (Inaba, 1957). The results of Experiment II showed the discrimination of small objects by raccoons to improve with experience.

The relevant experience may have been the learning of "supporting habits" (Riopelle, 1953), such as attention, the association of visual patterns with reward, or the withholding of response until the cues were analysed. Or it may have been some basic perceptual organisation that improved with practice, that is, within the visual apparatus itself.

In conclusion it can be stated generally that the raccoon can discriminate visually all test objects of any practicable size within the spatial limits of his manual reach. However, his separation acuity may be limited to a degree that interferes with any performance that depends on minute visual disentangling of adjoining stimulus materials. Nothing as yet can be said regarding raccoons' ability to discriminate more distant objects.

Summary

Two experiments were conducted to determine the visual discrimination abilities of raccoons in regard to materials used in testing in the Klüver-Wisconsin General Test Apparatus. Knowledge of these abilities is prerequisite to obtaining behavioural comparisons between raccoons and other species, particularly primates, which have been extensively tested using this apparatus.

Separation discrimination was tested by a chain pulling method, wherein the animals were required to draw in that one of two chains to which a food cup was attached. The distance between the chains was varied systematically. At a distance of 14″, raccoons discriminated intervals as small as $\frac{1}{4}''$. However, there was a progressive decrement in discrimination accuracy for intervals smaller than 3″.

The second experiment investigated the discrimination of very small objects. After a discrimination between two objects of 1″ maximum linear extent was learned, replications of these objects having a maximum linear extent of $\frac{1}{2}''$, $\frac{1}{4}''$, and $\frac{1}{8}''$ were presented. At a distance of five inches, all objects were successfully discriminated by all subjects, with no apparent differences from one size to another. It was concluded that raccoons are capable of discriminating visually the smallest sizes of objects that could be used practicably in this situation.

Furthermore, discrimination of all sizes of objects improved with experience.

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THE INFLUENCE OF EXPERIENCE ON THE BEHAVIOURAL EFFECTS OF ANDROGEN IN PREPUBERALLY CASTRATED MALE CATS*

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Although the concept of the dependency of sexual behaviour on gonadal hormones is well established in most vertebrates, functional interrelationships between hormonal output and behavioural mechanisms are often poorly understood. A case in point is the relatively long persistence of sexual behaviour after castration in males of a variety of vertebrate species. The explanation frequently proposed, that the adrenal gland is furnishing the required androgens, has not, however, been substantiated (Warren & Aronson, 1956, 1957; Cooper & Aronson, in ms.). On the contrary, sexual behaviour may sometimes proceed in the absence of androgen (Beach, 1947).

Recently, Rosenblatt & Aronson (1958) found that persistence of sexual behaviour after castration depends to a considerable extent upon the males having at least a small amount of mating experience before the testes were removed. In this experiment several male cats that had been permitted only a single mount with thrusting, failed to initiate any mating activities after castration. By contrast, most of the males permitted extensive preoperative sexual experience, continued sexual behaviour for extended periods. Although male cats seem to require androgens for the initiation of sexual behaviour, they are usually capable of sustaining this behaviour for considerable periods even when the androgen level is low or possibly zero. These results emphasise the importance of castration prior to puberty as a further step in the investigation of the relationship of sex hormones and sexual experiences to the initiation and maintenance of sexual behaviour.

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Experiments of this type have been carried out with rodents. Beach (1942, 1942a) with rats, and Warren & Aronson (1958) with hamsters have found that when tested in adulthood, some individuals show on occasion a rather high level of sexual behaviour, including the complete copulatory pattern, executed in a manner typical of the intact animal. Rats castrated when 21 days old, after treatment with testosterone propionate, all showed the complete pattern including ejaculation (Beach & Holz, 1946). Although comparable data for cats are not available, according to the phylogenetic considerations discussed by Beach (1947), the higher mammals with their more elaborate cerebral cortex are less dependent on gonadal hormones for performance of the sexual acts. From this hypothesis, it might be expected that prepuberally castrated cats would exhibit more sexual activity in adulthood than rodents similarly treated.

In the present experiment male cats that had been castrated prepuberally were later tested for sexual behaviour when they reached adulthood. At the time of test these males were not very responsive to the female, This fact was distinctly advantageous for later stages of the experiment where the influences of experience and hormone were tested. Following this first series of tests, all of the males were treated with testosterone propionate. During the period of treatment, some of the animals were permitted sexual contacts with females while others were denied such experiences. When androgen treatment was eventually terminated, the experienced males were tested for the persistence of sexual behaviour, while the deprived males were tested first for a possible advancement in sexual behaviour over their previous very low level, and second, to establish the degree of persistence and the level of sexual behaviour eventually attained. In these ways we hoped to learn whether the physiological changes produced by the sex hormones are in themselves sufficient to produce the mating pattern or whether additional ontogenetic processes (e.g. sexual experience) are also involved in the organisation of the behaviour.

To summarise our aims, the present study is directed to an examination of the following questions:

1. What is the effect of prepuberal castration on the appearance of sexual behaviour in adulthood?

2. Does the absence of endogenous androgen during the developmental periods of prepuberty and puberty reduce the effectiveness of administered androgen in inducing sexual behaviour in adulthood?

3. Does androgen administration in adulthood advance the organisation of the mating pattern in the absence of opportunity for sexual experience?

4. Will males that are permitted sexual experiences during the period of androgen therapy persist longer in sexual behaviour following hormone withdrawal than males that are not permitted contact with females during the treatment period?

Preliminary Experiment

Prior to the main experiment data were obtained on two cats primarily to determine (1) whether prepuberally castrated males will react sexually to females, (2) what may be the influence of androgens on the behaviour of these animals and (3) what age is appropriate for castration in our experiment.

One male, Eunie, was castrated when 3 months old. Between 3½ and 8 months, he was given many tests with groups of males and females of comparable age. During this period, he never showed any masculine sexual behaviour but on numerous occasions he was mounted* by other cats. Then between 18 and 32 months of age, at varied intervals, he was given 34 tests with one or more spayed females brought into heat by estrogen treatment,† The total of sex behaviour observed in all of these tests, was 4 short mounts and 3 very brief neck grips without mounts.

At the age of 3 years 3 months a 78 mg. pellet of testosterone propionate† was implanted subcutaneously into Eunie, who thereafter was tested once weekly. In the 8th week after implantation, he achieved his first neck grip with a female in the new test series. During the 13th week, on one occasion we observed a neck grip and mount with stepping and pelvic thrusting, but erection was slight and intromission did not follow. This mount was held for 12 minutes, and except for his inability to achieve intromission through inadequate erection, the movements and positions assumed were typical of normal males. Three more mounts were recorded but thereafter up to the 44th week, no more sexual behaviour was observed. At 4 years 2 months, we began a series of injections of 1 mg. per day of testosterone propionate, 6 times weekly. Later this was increased to 20 mg. per dose and was supplemented by a newly implanted pellet. Three weeks later, a short neck grip and mount was recorded; in the 22nd week, a 21-minute mount with stepping and thrusting appeared. During one of the tests in the 23rd week Eunie achieved his first intromission after a 13-minute mount. He was then 4 years 7 months old and had received approximately 2,300 mg. of testosterone during this series of hormone treatments. During the next 37 weeks Eunie achieved a total of 52 intromissions during 98 tests. Hormone treatment was then discontinued and the following results were obtained thereafter: 1st week—one intromission; 2nd week—in one test, a long mount with erection failing; 3rd and 4th weeks—many approaches to female; 5th to 7th week—no longer responsive to the female.

A second male, Smoky, was castrated when 6 months old. At 6-1/2 months he was tested but no sexual behaviour was observed. Between 1-1/2 and 3-1/2 years he was given 43 tests sometimes with more than one female present. During this series of tests we recorded 16 short mounts and 17 neck grips but no stepping, thrusting, or intromissions were observed. Smoky was then implanted with a 48 mg. pellet of androgen. Four weeks later he showed his first mount followed by an intromission. For the next 9 weeks Smoky had between 1 and 3 intromissions per test (total 14). The pellet was then removed and reweighed, showing a loss of 35·1 mg. in 12 weeks. After hormone withdrawal, Smoky continued to have 2 intromissions in almost every test for 7 weeks. From then until the 22nd week, intromissions were irregular and in addition there was evidence of weakening erections. Smoky continued to mount the test female until the 31st week and thereafter was unresponsive toward her.

These preliminary results indicate that untreated prepuberally castrated male cats exhibit very little sexual activity other than an occasional neck grip and mount. However, sexual behaviour can be induced by androgen treatment. The

*See page 173 for a list of behavioural items included in the mating pattern.

†The estradiol benzoate (Progynon-B) and testosterone propionate (Oreton) were kindly furnished by the Schering Corp., Bloomfield, N.J.

striking differences between Eunie and Smoky in the number of tests required and the amount of hormone needed to induce sexual behaviour would seem attributable at least in part, to a difference of 3 months in the ages of these two cats at castration.

In our earlier studies it was found that occasionally a male would exhibit the full mating pattern at 6 months of age, although the average age for a large group was around 11 months. Because only the behavioural criteria of sexual maturity were known at the beginning of the present study, castration was performed at the age of 4 months to eliminate the early physiological changes of puberty as a factor. However, since that time Aronson, Rosenblatt & Cooper (unpublished) have shown that hormonally controlled spines on the cat's penis start developing at 3 to 4 months. We must assume therefore that early effects of sex hormones may have been influential to some extent in the sexual behaviour of males in this experiment.

Materials and Methods

The main experiment started with 13 male kittens born in the laboratory, Two of these died from the effects of urinary blocks, after the first series of tests before hormone administration. Therefore the complete results are based on 11 subjects. These remained in excellent health except for occasional colds. All were vaccinated against feline panleucopenia (cat distemper) and booster inoculations were administered at yearly intervals.* The animals were housed in separate cages except for a period of about one hour each week when males and females of similar ages were left together in a room for exercise and free play. This procedure permitted the development of social relationships among the animals and also insured habituation to the room used later for the sex tests. Castrations were performed between the ages of 118 and 128 days. Tests for sexual behaviour were begun when the subjects were 332 days of age and continued until they were 503 days old.

The following items were recorded for each male during each 20-minute test period with a female in heat: (1) approaches (definite movements to the female); (2) partial, deviant and normal neck grips; (3) partial or complete mounts and their duration; (4) the occurrence of stepping, pelvic thrusting, and forepaw rubbing; (5) the frequency and duration of mounts terminating in intromission; (6) duration of intromission.

To provide a more comprehensive indication of sexual behaviour, a "single sex score" was developed by Rosenblatt & Aronson (1958) to represent the type of behaviour and the frequency of the various elements. These items of behaviour were weighted according to the completeness of the pattern. The scale follows:

Not responsive to the female	0 points
Attention to the female (e.g. definite movements toward the female, anal-genital sniffing)	1
One or more neck grips	2
One short mount (less than 1 minute)	3
More than 1 short mount or 1 medium mount (1-4 minutes)	4
More than 1 medium mount	5
One or more long mounts (4 minutes or longer)	6
Stepping movements	add 1 to above score
Pelvic thrusting	add 1 „ „ „
One intromission	9 points
Each additional intromission	add 1 to above score

For additional details on the care and housing of the animals, the exercise routine, the surgical procedures, the description of mating behaviour, methods of quantification and the sex score, the reader is referred to the prevous paper by Rosenblatt & Aronson (1958).

Procedure and Results

Part 1. Effects of Prepuberal Castration

Intact males start mating at the age of 333 days, on the average (Rosenblatt & Aronson, 1958). When the prepuberally castrated males reached this age (332 to 365 days) they were each given 10 sex tests spaced approximately two weeks apart. The data for these tests are summarised in Table I. Only one of the 13 animals mounted the female during this series of tests but even he did not perform stepping or thrusting. One additional male obtained typical (dorsal) neck grips and eight other males obtained deviant neck grips (ventral or lateral). Most of the males occasionally made definite "approaches" toward the female but two of the test animals never displayed even these preliminary elements of the sex pattern.

Among intact males, introductory sexual behaviour such as "approaches" and deviant neck grips, and even typical neck grips, rarely appears without the male subsequently taking a mount

*We wish to express our appreciation to the Lederle Laboratories, American Cyanimide Corporation, Pearl River, New York, for generous supplies of Feline Distemper Vaccine.

Table I. Sexual Performance of Prepuberal Castrates during Adulthood (332-503 days) but Prior to Hormone Administration

Animal	Average sex score		No. of mounts	No. of dorsal neckgrips	No. of ventral or lateral neckgrips	No. of "approaches"
	tests 1—5	tests 6—10				
Angus	3·2	0·6	14	9	7	17
Grisly	1·2	1·3	0	4	15	9
Charlie III	1·0	1·0	0	0	1	0
Charlie II	1·0	1·0	0	0	2	1
Bloat	1·0	1·0	0	0	1	3
Sleepy	1·0	0·8	0	0	6	10
Spotty	1·0	0·4	0	0	0	2
Fighter	1·0	0·0	0	0	4	1
Snowy	0·8	0·2	0	0	4	2
Puff	0·6	0·0	0	0	1	2
Charlie IV	0·4	0·6	0	0	7	3
Rusty	0·2	0·0	0	0	0	0
Charlie I	0·0	0·0	0	0	0	0
Mean	0·91	0·46				
S.D.	0·71	0·50				
	$P<·01$					

with neck grip and completing the mating pattern. These types of sexual behaviour, which represent the first indications of sexual arousal, are usually followed by increasingly frequent and progressively more complete performances of sexual behaviour (Rosenblatt & Aronson, 1958). An opposite trend appears in the group of prepuberal castrates where there was a gradual but significant decline ($P<·01$) in sexual behaviour from the first five tests to the last five tests.

Part 2. Effects of Administering Androgen in Adulthood to Prepuberal Castrates

When the previous series of tests were complete, androgen therapy was started. The males were divided into two groups, those receiving sex tests (Group I) and those not permitted sexual experience during the period of hormone administration (Group II). Each animal received injections of 20 mg. per day of testosterone propionate in sesame oil on Monday through Friday and 30 mg. on Saturday.

The animals of Group I were given 3 tests per week until they achieved intromissions in two successive tests. The performances of these males during this series of tests may be considered one measure of the effectiveness of hormones in eliciting sexual behaviour in males deprived of sex hormones during the developmental periods of prepuberty and puberty. After intromissions had been achieved in two successive tests, pellets of hormone weighing approximately 50 mg. were implanted subcutaneously, and administration of hormone by injection was stopped. Tests were reduced to one per week. This schedule was continued for a period of at least three months or until the animals maintained a fairly constant number of intromissions per test. During this period, pellets were replaced when on palpation they seemed reduced in size.

The hormonal regimen and results of the sex tests are summarised for this group in the upper part of Table II. Sexual behaviour could not be elicited from two of the six males notwithstanding the fact that they were given many tests, and that a large amount of hormone was administered (more than 3 grammes) over a long period.

Table II. Outline of Hormone Administration and Sex Tests

			Hormone Administration				Sex Behaviour Tests*						
			By injections		By pellet								
Group	Animal	Age† (days)	Total no. of injections‡	Total amt. (mg.)	Days implanted	Amt. absorbed (mg.)	Total no. of tests	No. of tests to 1st mount**	Amount of hormone to 1st mount with thrusting (mg.)	No. of tests to 1st intromission	Amount of hormone to 1st intromission (mg.)	Total no. of intromissions	Av. freq. of intromissions per positive test
I	Angus	487—578	12	260	76	39·80	17	2	80	5	220	30	2·54
	Grisly	491—621	27	580	97	21·50	46	3	110	13	540	134	4·75
	Puff	489—608	62	1310	46	18·97	48	24	1050	30	1290	43	2·93
	Bloat	489—873	43	925	333	93·32	72	9	410	24	1050	55	1·71
	Charlie II	488—613	160	3230	—§	46·00	No sex behaviour shown in 78 tests						
	Fighter	490—681	184	3750	—§	39·00	No sex behaviour shown in 95 tests						
II	Spotty	489—757	184	3750	84	25·50	Not tested during hormone administration						
	Charlie III	486—725	155	3150	84	48·00							
	Charlie IV	486—730	160	3230	84	45·00							
	Snowy	473—701	137	2970	91	31·00							
	Sleepy	489—822	27	580	306	127·35							

*Males given 3 tests per week up to the 2nd consecutive test in which intromission occurred. Thereafter they were given one test per week.
†From beginning to end of hormone administration.
‡Monday to Friday 20 mg/day; 30 mg. on Saturday.
**Before 1st intromission.
§Pellet not removed.

One of these males (Fighter) became extremely aggressive toward each of a succession of females used, while the second male (Charlie II) remained inattentive to all females presented. However, this ratio (2:6) is not significantly higher ($P = \cdot 50$) than that obtained for intact animals of comparable age, with seven out of 53 males tested in this laboratory for initiation of sexual behaviour, failing to show such behaviour.

The remaining four males showed a wide variability in the number of tests and the amount of hormone required to elicit the first mount and the first intromission. In these cases the mating pattern, when it appeared, could not be distinguished from that of intact males.

During the development of sexual behaviour in most normal males, intromission occurs in the same test as the first mount with thrusting. In all of the prepuberal castrates, by contrast, there was a considerable span of time and consequent increase in androgen received between the first mount with thrusting and the first intromission. This interval varied from 3 tests and 140 mg. of androgen in Angus to 15 tests and 640 mg. of androgen in Bloat. In our earlier study we had learned that failure in male cats to achieve intromission during mounts with thrusting is frequently symptomatic of inadequate erection. Observations during this experiment revealed that in at least two animals, Angus and Grisly, inadequate erections probably were the cause for the failure to achieve intromission during tests in which thrusting occurred.

After the period of androgen administration with the sex tests, the pellets were removed; then the four males were tested once each week starting on the seventh day after the hormone withdrawal. During the first 15 weeks (upper part of Table III), three of the males achieved intromission in several tests and all of the males continued to mount the female with pelvic thrusting in tests extending over several weeks. The only male that was unable to achieve intromission performed a long mount with persistent,

Table III. Number of Intromissions and Mounts in 15 Tests after Hormone Withdrawal

Group	Animal		Level before hormone withdrawal*	Tests after hormone withdrawal†														
				1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
I	Angus	I‡	3·0	2	2	2	2	3	2	2	3	2	1	1	0	1	2	0
		M**	1·2	5	6	4	9	2	1	1	0	4	2	5	2	1	2	1
	Grisly	I	4·0	1	3	1	1	0	0	0	0	0	0	0			0	0
		M	0·4	3	2	3	4	4	2	3	0	4	4	7			5	1
	Puff	I	3·6	0	2	1	0	0	0	0	0	0	0	0	0	0	0	0
		M	0·4	0	0	1	2	0	1	0	0	0	1	1	0	0	0	0
	Bloat	I	1·2	0	0	0	0	0	0		0							
		M	0·0	1	0	3	0	0	1		0							
II	Sleepy	I		0	0	0	0	0	0	0	0	0	0	0	0	0	0	
		M		0	0	2	15	0	7	7	2	1	0	0	0	1	0	
	Spotty	I		0	0	0	0	0	0	0	0	0	0	0	0	0		0
		M		0	0	0	2	0	0	0	1	0	0	0	0	1		0
	Charlie III	I	No Tests Given	0	0	0	0	0	0	0		0						
		M		0	0	0	0	0	0	0		0						
	Charlie IV	I		0	0	0	0	0	0	0	0		0					0
		M		0	0	0	0	0	0	0	0		0					0
	Snowy	I		0	0	0	0	0	0	0		0			0	0		
		M		0	0	0	0	0	0	0		0			0	0		

*Average of last 5 tests.
†1 test per week.
‡Intromissions
**Mounts not leading to intromission.

vigorous pelvic thrusting during the first test, suggesting that inadequate erection of the penis may have accounted for this failure.

In our earlier paper on the decline of sexual behaviour in a group of postpuberal castrates, three types of decline were distinguished in approximate ratio of 1:1:1. These were characterised in the following way: Type A males showed an initial decline in frequency of intromission without any loss of intromissive ability for periods ranging from 8 months to 3½ years, and mounting with thrusting persisted indefinitely after intromission ceased to appear. In Type B males intromissions ceased within 2 to 3 months but mounts, and occasionally thrusting, continued to appear in some cases for as long as 1½ years. Type C males ceased all sexual behaviour within a few weeks after castration and thereafter paid very little attention to the female.

These three types of decline occurred among the experienced males of Group I of the present experiment in a ratio of 1:1:2. Examples of these are illustrated in the graphs of Fig. 1 in which changes in sex scores are compared with the equivalent types among the postpuberal castrates. Thus the prepuberal castrates showed the same kind of variations as postpuberal castrates in the retention or decline of sexual behaviour when the androgen level was reduced. A comparison of the data from the two experiments suggests that Type A males of the postpuberal group retained the ability to achieve intromission for longer periods than the single type A male of the prepuberal castrate group. The samples are too small, however, to permit definite conclusions on this point.

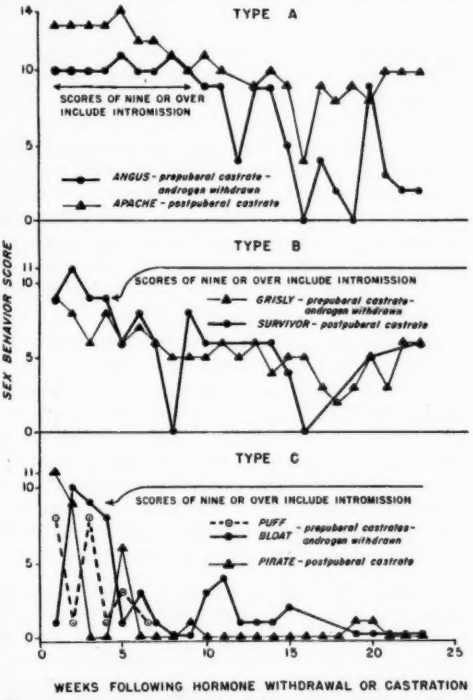
TYPE A
SCORES OF NINE OR OVER INCLUDE INTROMISSION
ANGUS - prepuberal castrate - androgen withdrawn
APACHE - postpuberal castrate
TYPE B
SCORES OF NINE OR OVER INCLUDE INTROMISSION
GRISLY - prepuberal castrate - androgen withdrawn
SURVIVOR - postpuberal castrate
TYPE C
SCORES OF NINE OR OVER INCLUDE INTROMISSION
PUFF
BLOAT
- prepuberal castrates - androgen withdrawn
PIRATE - postpuberal castrate
SEX BEHAVIOR SCORE
WEEKS FOLLOWING HORMONE WITHDRAWAL OR CASTRATION

Fig. 1. Decline in sexual behaviour of androgen-treated prepuberal castrates after hormone withdrawal, compared with decline of males after postpuberal castration. The comparisons also illustrate the three types of decline. Data on postpuberal castration from Rosenblatt & Aronson (1958).

Part 3. Effects of a Period of Androgen Administration Without Sexual Experience on the Nature of Sexual Performance after Hormone Withdrawal.

In the series of tests carried out prior to hormone administration, the level of sexual behaviour shown by the five males of Group II did not exceed occasional deviant neck grips in addition to several "approaches." The largest number of these types of behaviour shown by a single male (Table I) was a total of 6 deviant neck grips and 10 "approaches" during 10 tests.

At the conclusion of this series of tests, androgen was administered to each animal both by injection and by pellet implantation and these males were permitted to exercise in the testing room for periods equivalent to the length of the sex tests. We had intended to give the animals of Group II an amount of hormone equal to the largest amount required to initiate sexual behaviour in the males of Group I. However, the failure of two of the animals of that group, Fighter and Charlie, to mate even after receiving very large doses of androgen, necessitated maintaining the six males under hormone treatment for an average of 260 days. This procedure was necessary in order to match the period of treatment of the two unresponsive animals. As shown in the lower part of Table II the total amount of hormone received by all but one of these males far exceeded the amount received by the sexually active males of Group I. In addition to daily injections of androgen the males of Group II were implanted with pellets in order to match the procedure followed with Group I.

Seven days after the end of hormone administration in Group II, a series of weekly sex tests was started. Results of the first 15 tests of this

series, presented in the lower part of Table III, show that hormone administration alone was completely ineffective in advancing the sexual performance of three of the five males. Definite advances were shown by two males. Although Spotty had shown only "approaches" during tests prior to hormone administration, he now performed short mounts without arching of the back, stepping or thrusting. Sleepy, after the long period of hormone administration, showed changes in sexual performance which were even more significant. Mounting behaviour appeared for the first time during the third week and increased in frequency during succeeding weeks. Stepping movements also appeared during the third week, and in the sixth week both stepping and thrusting were shown. The highest development of sexual behaviour by this male was shown in the sixth and seventh weeks when long mounts with thrusting were performed. Intromissions did not appear, probably due mainly to lack of erection or bending of the penis upon contact with the female's hind region during thrusting. Inadequate erections were confirmed by close observation of the penis during these long mounts.

Although the advances in sexual behaviour made by these two males can be attributed in the main to an intervening period of hormone administration, the influence of experience gained in the first few tests after hormone withdrawal cannot be excluded. In both animals there were initial tests in which no elements of sexual behaviour appeared in advance of those shown prior to hormone treatment. Spotty required four tests to achieve his first mount, and Sleepy required three prior tests before the first mount and stepping appeared, and three more tests including 18 additional mounts before thrusting appeared.

Part 4. Effects of Androgen Administration alone Compared with Effects of Androgen Administration Concurrent with Sexual Experience on the Performance of Sexual Behaviour after Hormone Withdrawal

In an earlier experiment (Rosenblatt & Aronson, 1958) sexually experienced males persisted in sexual behaviour after castration for longer periods and at a higher level than males either permitted only a single mount or deprived of all sexual experience prior to the operation. Results of the present experiment with prepuberal castrates confirm this earlier result. In Fig. 2 the sex scores of experienced and inexperienced

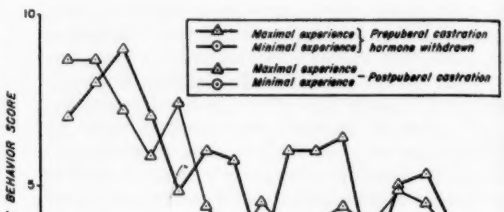

Fig. 2. Average sex behaviour scores for first 15 weeks following (1) hormone withdrawal of androgen-treated prepuberal castration, (2) postpuberal castration, among (3) males permitted maximal prior sexual experience, and (4) males permitted only minimal sexual experience.

males after hormone withdrawal are compared with similar scores for experienced and inexperienced males castrated in adulthood. The close conformity of the average sex scores for the two groups of sexually experienced males and the two groups of inexperienced males suggests that both the sexual experience gained in the presence of normally secreted endogenous sex hormone and that gained during administration of exogenous hormone are equally effective in their influence on persistence of this function after decline in hormone level.

A comparison of the percentage of animals attaining either a mount or intromission during each of the first 15 tests after castration or after androgen withdrawal showed a decided difference between experienced and inexperienced males of the two experiments and a slightly greater percentage for the postpuberal castrates than for the prepuberal castrates. However, the small size of the groups permits no definite conclusions as to the reliability of the difference.

A lack of extensive sexual experience under either condition of hormone introduction is equally detrimental with respect to the persistence of sexual behaviour after decline in hormone level. Apart from a difference between pre- and postpuberal castrates in the persistence of intromissive behaviour mentioned earlier (p 177), no other difference between animals in the two experiments can be assigned to the difference in age of castration.

Discussion

The results of the present experiment and of the earlier experiment previously reported (Rosenblatt & Aronson, 1958) show that most sexually experienced male cats will continue to perform all or part of the sexual pattern for a considerable time after the source of male hormone has been removed (Part 4). The same effect is produced by the removal of naturally occurring testicular secretion as by the cessation of exogenous androgen administration. Our findings on persistence are therefore in agreement with those of many other investigators of mammalian sexual behaviour. Nevertheless a tendency has existed to minimise the above point and instead to postulate a direct relationship between amount of hormone and amount of sexual behaviour.

The present experiment also shows that adult cats are unlikely to initiate sexual behaviour in the absence of male hormone (Part 1). This matter apparently differs in other mammals, and we shall return to this point. The fact remains, as part two of this paper shows, the introduction of male hormone will rapidly induce a full pattern of sexual behaviour in most adult male cats. The seemingly contradictory evidence presented above, namely, an ability of sexually experienced males to continue sexual behaviour after castration, in contrast to a limited ability of prepuberal castrates to develop sexual behaviour, must be resolved theoretically for better understanding of the entire problem. Schneirla (1956) has provided a general theoretical background permitting us to understand how progressive changes occur during ontogeny in the physiological and psychological organisation of behaviour patterns. Particularly relevant are the relationships of intrinsic and extrinsic factors including experience, and how these may interact under the conditions of development. Along these lines Lehrman (1956) reviewed the influence of experience in the rise and change of parental behaviour in birds and mammals. Specifically in relation to reproductive function, Beach (1948) states that the characteristics of endocrine-influenced physiological mechanisms may be altered by the experience of the individual.

In the interpretation of our experiments it is crucial to distinguish between the initiation of sexual behaviour by a male, normally occurring during puberty, and the continued performance of sexual behaviour after this period. Since the transition from absence of mating behaviour to its initial performance in partial or complete form is, in the majority of male cats, associated with the presence of hormone and the opportunity to display sexual behaviour toward a receptive female, a careful analysis is necessary before adequate conclusions can be drawn as to the role of the male hormone.

In the writing of contemporary investigators, two possibilities are suggested as to the types of mechanisms by which hormones induce sexual behaviour. Several hypotheses (Bard, 1940; Beach, 1942; Tinbergen, 1951; Fisher, 1956) propose a "direct" influence of hormones on centres in the nervous system in which are organised the neural circuits controlling mating behaviour. The exact nature of hormonal effects may be either "sensitizing" or "potentiating" according to different hypotheses. In contrast, several other investigators (Beach, 1951; Grunt & Young, 1953; Valenstein, Riss & Young, 1955) take into account the multiplicity of physiological and morphological changes caused by androgens, including those presumably occurring in the central nervous system, in order to describe what type of organic condition might underlie the appearance of sexual behaviour. The totality of these changes provide the organic setting for the development of the particular behavioural sequence involved in the mating pattern. Additional conditions and further changes are required for the organisation of the mating pattern and these are accomplished during the initial series of sexual contacts. This type of theory makes one of its chief contributions by indicating an important but indirect influence of androgen on sexual behaviour, in contrast to the more direct action proposed above.

It is possible to test each of the views presented above by determining the effects of hormone administration independent of the effects of sexual experience. Objections can be raised against the procedure of testing an animal for the initial appearance of sexual behaviour under hormone administration. Conceivably, sexual experience may exert its effects with extreme rapidity so that they may be overlooked or even discounted, particularly when the influence of experience is effective concurrently with hormone administration. A second difficulty is raised when items of sexual behaviour make their appearance gradually. It may seem reasonable to attribute this either to a gradual increase in the amount of circulating hormone or to a gradual development of sensitisation or poten-

tiating effects in the central nervous system. The latter interpretations seem to derive support from the results of a number of experiments (Beach, 1947a) in which males have been castrated and have gradually lost sexual behaviour in an order which is the reverse of that in which the elements of sexual behaviour appear during development.

To deal with the problem of how hormone administration contributes to the organisation of the sexual pattern a special technique was developed. The sexual behaviour of an animal after hormone was withdrawn was used as an index of the status of sexual organisation present when hormone was being administered in the absence of concurrent sexual experience. As the present experiment (Part 4) and the one previously reported have demonstrated, the performance of sexual behaviour before castration or before hormone withdrawal is correlated with its appearance postoperatively. Similarly, failure to perform sexually at this time is correlated with absence of sexual opportunities at an earlier time when hormone was present.

Although no sexual behaviour in tests after hormone withdrawal was shown by three of the males given androgen treatment but no contact with females (Part 3), conceivably they could have been capable of mating while under hormone treatment through the influence of androgen alone. However, testing them during the period of hormone administration would have defeated the purpose of the investigation which is to estimate the influence of androgen alone on the organisation of sexual behaviour.

Fortunately, an experimental distinction can be made between animals who have not yet developed the mating pattern at all as far as can be determined and animals who have developed it through earlier experience, but do not evince it under present conditions. This was accomplished by administering adequate amounts of testosterone propionate to males of two groups with considerable past sexual experience during a period long after castration when sexual activity had declined to a low level (Cooper, unpublished). One group was permitted additional sexual contacts during the period of androgen administration, the other group did not receive such experiences. In tests after hormone withdrawal, these two groups were similar in their level of sexual activity, but more important, this level was considerably higher than that of males in our present experiment (Part 3), permitted only the minimal introductory sexual contacts before hormone withdrawal. Since both groups of previously experienced males showed considerably more sexual behaviour than the inexperienced males, performance after castration is considered to give a valid basis for estimating the status of sexual organisation before castration.

The analysis presented above supports an "indirect" influence of hormones during the period when sexual behaviour is being initiated. In addition to the organic changes caused by male hormone, it is clear that, for the cat, the experiencing of environmental stimuli must play an indispensable role in behaviour promoting the development of the mating pattern. Once organised through experience, this pattern becomes partly independent of the hormone. However, in the absence of androgen, regressive physiological and morphological changes eventually disrupt the pattern. On the other hand, when there has been no opportunity for sexual experience during the period of puberty (or hormone administration to prepuberal castrates), no further advances in the organisation of the sexual pattern occur, and as a consequence after hormone depletion sexual behaviour seldom is initiated.

However, two exceptional cases (Part 3) indicate that the situation is more involved. After androgen withdrawal, two prepuberally castrated males (not tested during hormone treatment) showed definite advances in sexual behaviour over their very low pre-treatment level. The fact that a protracted period of testing was necessary for this behaviour to appear, indicates a strong likelihood that the first sexual experience gained after hormone withdrawal was important for these further advances. This raises the possibility that the organic changes normally induced by androgens may recede gradually after hormone withdrawal, thus providing the setting for a partial organisation of the mating pattern before the organic effects have disappeared.

The technique of prepuberal castration and hormone administration provided additional information on the general role of androgen during development. When prepuberal castration is performed at three months of age, the influence of sex hormone is eliminated during the subsequent seven month period prior to the average age of normal sexual maturity (Part 2). Yet within a few tests after the start of hormone treatment, sexual behaviour appeared in one male and it appeared in three more males during subsequent tests. Moreover the full mating pat-

tern, when it appeared in these four males could not be distinguished from that performed by intact males. Furthermore, the three characteristic types of decline in sexual behaviour after castration, as described in our previous report, were also found after hormone withdrawal in the prepuberal castrates (Part 4). These results suggest that for the majority of males, the appearance of sexual behaviour at puberty does not depend upon the presence of sex hormones during the immediately preceding period. That is, the physiological background for the appearance of sexual behaviour, which is normally established by the rising level of androgen during the period of puberty, can be postponed under experimental conditions to a later time.

In two other respects the prepuberally castrated males treated with androgen appeared to differ from intact males. The span of tests between the first thrust and the first intromission was greater on the average in the group of prepuberal castrates than among intact males. In two cases, erections during the first mounts with thrusting were either too small to permit intromission, or the penis bent upon contact with the female's hind region. Among intact males the first thrusts usually lead to intromission during the same mount. The second difference was the limited persistence of intromissive ability after hormone withdrawal. Differences in penis development between pre- and postpuberal castrates could lead to an early loss of erectile ability in the early castrates, thereby accounting for the reported difference in persistence.

In his phyolgenetic analysis of the hormonal and neural control of sexual behaviour in male animals, Beach (1942, 1947, 1947a) proposed the concept of an organised multisensory stimulus integrated in the central nervous system, probably in the forebrain. This multisensory effect is presumed to facilitate neural circuits which mediate the sexual responses. From a variety of evidence including the appearance of sexual behaviour in prepuberal castrates, Beach has generalised that in the ascending levels within the mammalian order, the direct importance of the gonadal hormones to sexual behaviour tends to decrease, whereas cerebral cortical influences increase.

While we find ourselves broadly in agreement with Beach concerning the probability of changing hormonal-CNS relationships among mammals, from our evidence it must be added that in higher mammals an increase seems to have occurred in the extent to which there is a specific dependence upon androgen for the development of sexual behaviour at puberty. Although problems and limitations arise when one attempts to compare levels of sexual behaviour of different species (Rosenblatt & Aronson, 1958), we are confident that the quantity and quality of sexual behaviour performed by our adult, untreated prepuberally castrated males, was far less than reported in comparable groups of rats (Beach, 1943, Beach & Holz, 1946), guinea pigs (Sollenberger & Hamilton, 1939; Seward, 1940; Riss, Valenstein, Sinks, & Young, 1955), and hamsters (Warren & Aronson, 1957).

Evidence from primates concerning the effects of prepuberal castration on developmentof sexual behaviour does not permit us to establish a phylogenetic relationship. In a single published record of the sexual behavior of a chimpanzee castrated before puberty (Clark, 1945) it is not possible to determine whether copulatory behavior ever occurred *before* testosterone therapy had been initiated. In the absence of evidence on the effects of prepuberal castration on the sexual behavior of animals standing at different level in the phyletic scale, Beach's evolutionary hypothesis cannot be adequately evaluated at this time.

Summary

Thirteen male kittens were castrated at the age of 4 months. When tested in adulthood with oestrous females they performed very little sexual behaviour. Only one of these males mounted the female, but stepping, thrusting and intromission were absent. When the above tests were completed, 11 of the males were treated with testosterone propionate by injection and pellet implantation. Six males (Group I) were permitted sexual experiences during the period of hormone administration. Of these, four showed the complete sexual pattern after relatively large doses of androgen. The other two never approached the female even after receiving over 3 gr. of hormone.

Five other males (Group II) were denied access to the female during the period of androgen therapy. After the hormone treatment was terminated, these animals were tested with a female. Three of these showed no advances in sexual performance over their low levels before androgen therapy started; two made definite advances during the period of testing, pointing to the importance of the experiences gained during the early tests after hormone therapy terminated. Also, the persistence of sexual behaviour after

hormone withdrawal was much greater among the maximally experienced males of Group I than among the minimally experienced males of Group II.

An analysis of the data from these experiments emphasises the distinction between initiation of sexual behaviour during ontogenesis, and the persistence of the organised sexual pattern when the androgen level is reduced. The data also favour the interpretation of an indirect influence of male hormone when sexual behaviour is being initiated. Androgen causes a variety of critical organic changes, but in addition, stimuli must be present in the environment which elicit behaviour tending to the development of the mating pattern. Once organised through hormones and experience, this behaviour remains for a time relatively independent of the hormone until such time as regressive morphological and physiological changes disrupt it.

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RANK ORDER IN CAGED RATS

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Introduction

Previous estimates of rank order in laboratory mammals have been undertaken in most instances by methods which take no account of the social environment and all of which involve interference with the animals. Thus, Ginsberg & Allee (1942), Seward (1945) and Scott (1948) kept their animals individually and brought them together in pairs for ranking. Baron, Stewart & Warren (1957) kept their cats in groups and abstracted pairs for ranking. These methods do not take into account much relevant knowledge of mammalian behaviour from which it can be seen that formation of hierarchies develops in a closed community within which the animals are in continuous social intercourse.

Such communities exist within a limited space whether the territory is fixed by physical boundaries or the space occupied by the groups is determined by the social characteristics of the particular animal. When the social characteristics set the boundaries to the community, the community as a whole may be nomadic as in a herd of ungulates or, as in monkeys, the social group may roam its territory.

Rank order in these communities or in those limited by territorial boundaries is thus part of the social structure and should, therefore, be studied in relation to this. Any adequate method of assessment should avoid interfering with the social behaviour of the animal. It has been found possible to do this by observing communities of caged rats.

The particular aspect of the individual behaviour which has been utilised in determining rank order was chosen on the following grounds, some of which have influenced the methods used by previous workers.

(1) Priority of access is widely considered the criterion of dominance and has usually been measured by priority of access to the incentive appropriate to an activated drive, e.g. food or the opposite sex. Dominance, however, results in priority of access in feeding or in sexual relations as a consequence of an established order of rank; thus, the process of setting up rank order is a necessary precursor to other overt evidence of dominance.

(2) Priority of access can be assessed between two individuals in direct social encounters when one of the animals adopts a submissive posture to the approach of another animal. This type of encounter gives evidence of order of rank.

(3) Social groups of monkeys are organised round an established order of males (Chance, 1956) which is constant over long periods of time; thus if the resolution of individual encounters exhibits stability or the order becomes more marked with time, this may be taken as an indication of the existence of dominance.

These points make it clear that the more fundamental aspect of rank order is the resolution of individual encounters and the persistence of the order so revealed. We wished to find a method for obtaining information on these two points by simple observation of the behaviour so that the information about rank order could be related to other contemporaneous aspects of the social structure. Here, however, we are concerned merely to report a method by which rank order may be assessed.

Methods

As the rat is nocturnal and normally asleep or quiescent during the day, some method of arousal had to be found. Entering the observation room or handling the animals did not rouse the rats enough. If, moreover, they were transferred to a new clean cage the majority of the time before resuming sleep was spent in exploring the cage. If, however, only the sawdust was renewed and the rats replaced in their original cage, exploration of the cage dominated behaviour for only a few minutes and was immediately followed by 10-15 minutes of social behaviour. The prominent feature at this stage was social exploration, when encounters between pairs of rats are easily distinguished.

An alternative method used here was to bring the active phase into the daylight hours by placing a continuous red light in the room and arranging for a bright white light to be switched on overnight, so reversing the activity rhythm. This is effective within a fortnight and enabled

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three times as much information on the average to be obtained by observing the rats for the same period in red light.

As several cages were under observation for the same period, it was necessary to randomise the order in which they were observed on any one day in order to eliminate any effect on the size of the sample of short periods of spontaneous activity which tended to occur during the morning.

In red light each cage was observed for thirty minutes and a record was made of the relevant parts of the behaviour. Individual rats were made readily distinguishable by marking on the head, back or rump with a commercial black hair dye.

The rats were drawn from a random-breeding Wistar colony shortly after weaning and members of each litter were caged together with members of other litters. The cages measure $15\frac{1}{2}''$ x $10\frac{1}{2}''$ x $8\frac{1}{2}''$ high.

Results

Description of Encounters Between Rats

From time to time during the period of observation one rat will be seen on its back with the head and forelimbs, or the whole of another rat, on top of it. The rat lying on its back has reached the final submissive posture, although the degree of submission presented to the opponent can vary according to the presence or absence of accompanying movements. This submissive posture is adopted eventually by one rat after an encounter with another and is recorded as an encounter resolution for assessing rank order (the rat showing this posture is scored as losing). It has been found that it is frequently the outcome of moving away and being pursued, turning away the head or following a break away from a defensive movement or posture, that is any movement, or intention movement, of flight. (See Plate II). This posture may also be adopted directly after a rat has been pounced on by another; usually this pouncing is from the flank but in older rats from the front.

These encounters, which are a prominent part of the play of young rats, continue into the adult life of caged rats, but become less frequent. That these are fights at a low level of intensity may be deduced by a comparison of the movements and postures with those seen when a male intruder is attacked by the home animals of an established community. In these encounters with an intruder the nipping may be quite severe and, in many cases, the intruder will retaliate. The attacker continues, however, until the full submissive posture is shown, or until the intruder asserts his dominance by threat postures which induce the rats of the home cage to retire.

Assessment and Stability

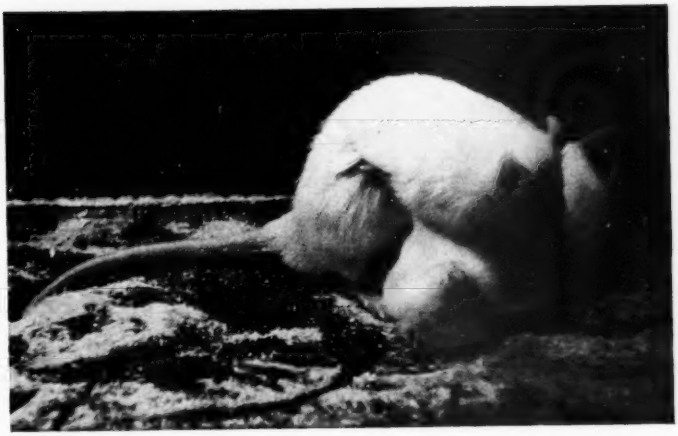
The tables are set out as follows. Along the top and down the left side are the individual rat numbers, not in order of rank but as marked at the beginning of the experiment. Each rat is then represented by a row and a column. In the row is the number of encounters it won against each other rat and in the column the number of encounters it lost against each of the other rats. For example, in the first cage of males, in the first period of observation, Rat 1 beat Rat 2 twenty-two times and lost to Rat 2 four times, and in the second period, Rat 1 won nine out of eleven encounters with Rat 2. For accurate ranking each pair should be inspected in this manner and this has been done for all cages by us and confirms the existence of a *linear* order for all cages of males except cages of six and some of the cages of females. A reasonable estimate can be formed by totalling the columns and rows and taking the ratio between totals of row and column for each rat.

A preliminary test was made to discover the influence of the number of rats per cage. Two, three, four, five and six rats were put into cages and each cage was observed three times per week over a period of three weeks. The encounter resolutions observed were tabulated at the end of the three-week period. The groups of three, four and five animals all showed a clearly defined order at the end of that time. The members of the pair remained of equal status; one animal won 19 encounters, the other 23.

A further test (Table I) revealed no rank order in cages of 6 rats even after a lapse of time. This is shown not only in the absence of any disparity in wins between individual rats but by the absence of a rat which beats all other rats or loses in all social encounters. In the cages containing 4 rats an order appeared in the first three weeks and with a few changes of position remained present in the final three weeks. A distribution was apparent at the end of the test between members of the pairs. It seems, therefore, that rank order appears in cages containing less than 6 rats.

We, therefore, had the choice of using groups of three, four or five animals for further work and as a group of four animals lay in the middle of the range showing rank order, we decided on this number.

PLATE II



A resolved encounter; the rat on the right is in the final submissive posture.

The next point investigated was the stability of the pattern. This was assessed by observing the cages for three weeks, then leaving them for three weeks, followed by a further series of observations for a final three weeks. Again, each cage was observed nine times in each of the three-week periods. Nine cages of males were observed in this way in normal lighting conditions. The encounter resolutions observed in each cage were tabulated at the end of each period; the ranking so found could then be compared between the two periods (Tables I & II).

As was stated in the section on methods, a certain amount of work has been done in conditions of a reversed light cycle. Here the experimental procedure was different; as there was no need to rouse the animals the amount of time spent on any cage each day could be increased. The time spent in observation was approximately the same for each test. The length of time for which each cage was observed at one stretch varied from test to test, but was the same within a test. The total period of observation was also reduced to two fortnightly periods with a two-week interval. Three more cages of males (Table III) were assessed in the same way and also ten cages of females, again in groups of four (Table IV).

At present the details of a statistical method suitable for estimating the degree of stability in a group by assessing the change in position of each animal between two observations has not yet been completed (Chance, M. R. A. & Waterhouse, J. A. H., in preparation). In Tests 4, 9 & 12 the data for the males showed that the rat at the bottom of the scale remained constant in 11 out of 12 cases and the most dominant rat in 7 out of 12. The expected stability of these positions, if random order be assumed, is one in four (the position may be occupied by any one of the four rats), which would be 3 times out of 12 in both instances. Assuming that the factors

Table I. Experiment in Daylight. (Males two, four and six in a cage). Test 4.

Resolved Encounters

1st period

Rat no.	1	2	Rank order
1		42	2
2	48		1

Rat no.	1	2	Rank order
1		60	1
2	52		2

Rat. no.	1	2	Rank order
1		17	1
2	12		2

Rat no.	1	2	Rank order
1		69	1
2	57		2

2nd period

Rat no.	1	2	Rank order
1		37	1
2	17		2

Rat no.	1	2	Rank order
1		11	2
2	26		1

Rat no.	1	2	Rank order
1		8	1
2	7		2

Rat no.	1	2	Rank order
1		18	1
2	14		2

Cage IV/2

1st period

Rat no.	1	2	3	4	Wins	Rank order
1		22	10	20	52	1
2	4		2	9	15	4
3	9	3		7	19	2
4	11	14	2		27	3
Losses	24	39	14	36	113	Total

2nd period

Rat no.	1	2	3	4	Wins	Rank order
1		9	2	5	16	2
2	2		1	6	9	4
3	18	7		14	39	1
4	2	10	4		16	3
Losses	22	26	8	25	80	Total

Cage IV/3

Rat no.	1	2	3	4	Wins	Rank order
1		8	10	1	19	3
2	3		3	1	7	4
3	16	9		1	26	1
4	1	3	1		5	2
Losses	20	20	14	3	57	Total

Rat no.	1	2	3	4	Wins	Rank order
1		2	4	4	10	4
2	3		1	3	7	3
3	5	2		2	9	1
4	7	4	1		12	2
Losses	15	8	6	9	38	Total

Cage IV/4

Rat no.	1	2	3	4	Wins	Rank order
1		14	18	9	41	2
2	2		0	2	4	4
3	19	3		6	28	1
4	0	3	1		4	3
Losses	21	20	19	17	177	Total

Rat no.	1	2	3	4	Wins	Rank order
1		5	4	6	15	2
2	1		1	8	10	4
3	8	4		5	17	1
4	3	4	1		8	3
Losses	12	13	6	19	50	Total

Cage I

Rat no.	1	2	3	4	5	6	Wins
1		1	4	0	3	4	12
2	4		6	0	0	1	11
3	5	6		0	1	5	17
4	0	0	0		1	0	1
5	4	1	0	0		2	7
6	3	6	3	0	4		16
Losses	16	14	13	0	9	12	Total 64

Rat no.	1	2	3	4	5	6	Wins
1		5	6	4	3	6	24
2	6		2	7	1	1	17
3	1	6		1	0	5	13
4	1	3	0		0	1	5
5	0	0	0	1		2	3
6	6	7	2	2	1		18
Losses	14	21	10	15	5	15	Total 80

Cage II

1st period

Rat no.	1	2	3	4	5	6	Wins
1		10	4	6	1	2	23
2	8		0	5	2	0	15
3	4	3		4	0	2	13
4	8	4	1		1	7	21
5	1	3	0	2		0	6
6	5	4	0	12	0		21
Losses	26	24	5	29	4	11	Total 99

2nd period

Rat no.	1	2	3	4	5	6	Wins
1		3	2	3	0	1	9
2	3		0	3	1	8	15
3	1	2		6	0	4	13
4	11	6	8		1	7	33
5	0	4	0	3		3	10
6	2	6	6	5	0		19
Losses	17	21	16	20	2	23	Total 99

Cage III

Rat no.	1	2	3	4	5	6	Wins
1		11	5	11	5	4	36
2	5		1	11	2	1	20
3	1	1		4	0	0	6
4	5	8	1		1	9	24
5	4	5	2	2		2	15
6	9	3	6	1	3		22
Losses	24	28	15	29	11	16	Total 123

Rat no.	1	2	3	4	5	6	Wins
1		1	5	1	1	0	8
2	1		3	1	0	0	5
3	7	2		0	2	3	14
4	0	2	3		3	3	11
5	0	3	0	1		0	4
6	0	3	0	1	0		4
Losses	8	11	11	4	6	6	Total 46

Cage IV

Rat no.	1	2	3	4	5	6	Wins
1		6	7	1	9	0	23
2	8		2	6	12	4	32
3	4	5		3	0	2	14
4	1	1	0		0	1	3
5	5	8	0	0		0	13
6	5	5	0	2	0		12
Losses	23	25	9	12	21	7	Total 97

Rat no.	1	2	3	4	5	6	Wins
1		3	2	9	13	1	28
2	0		0	5	0	1	6
3	2	1		2	0	1	6
4	4	4	1		9	4	22
5	1	2	1	0		0	4
6	0	3	1	0	1		5
Losses	7	13	5	16	23	7	Total 71

Table II. Experiment in Daylight (Males four in a cage). Test 9.
Resolved Encounters—Males

Cage A

1st period

Rat no.	1	2	3	4	Wins	Rank order
1		0	0	0	0	4
2	6		4	2	12	3
3	3	14		6	23	2
4	6	5	9		20	1
Losses	15	19	13	8	55	Total

2nd period

Rat no.	1	2	3	4	Wins	Rank order
1		0	0	0	0	4
2	1		0	0	1	3
3	5	1		3	9	1
4	1	2	0		3	2
Losses	7	3	0	3	13	Total

Cage B

Rat no.	1	2	3	4	Wins	Rank order
1		8	7	6	21	3
2	0		5	6	11	4
3	13	20		3	36	2
4	11	8	10		29	1
Losses	24	36	22	15	97	Total

Rat no.	1	2	3	4	Wins	Rank order
1		8	12	7	27	2
2	1		3	0	4	4
3	13	6		5	24	1
4	4	0	1		5	3
Losses	18	14	16	12	60	Total

Cage C

Rat no.	1	2	3	4	Wins	Rank order
1		16	13	16	45	2
2	4		2	3	9	3
3	15	5		11	31	1
4	10	1	5		16	4
Losses	29	22	20	30	101	Total

Rat no.	1	2	3	4	Wins	Rank order
1		8	2	3	13	2
2	6		4	2	12	3
3	3	7		10	20	1
4	2	0	3		5	4
Losses	11	15	9	15	50	Total

Cage D

Rat no.	1	2	3	4	Wins	Rank order
1		2	14	6	22	4
2	13		15	3	31	3
3	29	24		16	69	1
4	8	5	11		24	2
Losses	50	31	40	25	146	Total

Rat no.	1	2	3	4	Wins	Rank order
1		1	6	0	7	4
2	8		6	1	15	3
3	20	10		2	32	1
4	1	3	0		4	2
Losses	29	14	12	3	58	Total

Cage E

1st period

Rat no.	1	2	3	4	Wins	Rank order
1		1	2	4	7	4
2	8		11	5	24	2
3	6	7		3	16	3
4	17	6	6		29	1
Losses	31	14	19	12	176	Total

2nd period

Rat no.	1	2	3	4	Wins	Rank order
1		1	1	1	3	4
2	10		9	8	27	1
3	2	3		0	5	3
4	1	4	0		5	2
Losses	13	8	10	9	40	Total

Cage F

Rat no.	1	2	3	4	Wins	Rank order
1		10	2	0	12	4
2	10		12	2	24	2
3	7	3		0	10	3
4	5	13	7		25	1
Losses	22	26	21	2	71	Total

Rat no.	1	2	3	4	Wins	Rank order
1		3	1	1	5	4
2	8		2	3	13	2
3	2	1		0	3	3
4	3	4	1		8	1
Losses	15	8	4	4	29	Total

Table III. Experiment in Reversed-light Cycle (Males four in a cage). Test 12

Resolved Encounters—Males

Cage IV/1

1st period

Rat no.	1	2	3	4	Wins	Rank order
1		21	32	30	83	1
2	9		14	18	41	2
3	6	13		28	47	3
4	4	10	22		36	4
Losses	19	44	68	76	207	Total

2nd period

Rat no.	1	2	3	4	Wins	Rank order
1		8	25	17	50	1
2	7		3	10	20	2
3	17	13		15	45	3
4	5	8	14		27	4
Losses	29	29	42	42	142	Total

Cage IV/2

Rat no.	1	2	3	4	Wins	Rank order
1		20	52	33	105	2
2	42		37	24	103	1
3	10	10		18	38	3
4	3	7	3		13	4
Losses	55	37	92	75	259	Total

Rat no.	1	2	3	4	Wins	Rank order
1		30	23	18	71	1
2	12		31	21	64	2
3	12	27		18	67	3
4	3	21	14		38	4
Losses	27	78	68	57	240	Total

Cage IV/3

1st period

Rat no.	1	2	3	4	Wins	Rank order
1		58	23	20	101	1
2	23		15	4	42	3
3	5	10		6	21	4
4	3	10	23		36	2
Losses	31	78	61	30	200	Total

2nd period

Rat no.	1	2	3	4	Wins	Rank order
1		39	20	23	82	1
2	22		14	18	54	2
3	2	7		5	14	4
4	19	13	11		43	3
Losses	43	59	45	46	193	Total

Table IV. Experiment in Reversed-light Cycle (Females four in a cage). Tests 11 and 12.

Resolved Encounters—Females

Test 11

Cage I

1st period

Rat no.	1	2	3	4	Wins	Rank order
1		1	3	6	10	4
2	5		3	3	11	3
3	10	5		0	15	2
4	10	10	3		23	1
Losses	25	16	9	9	59	Total

2nd period

Rat no.	1	2	3	4	Wins	Rank order
1		0	4	3	7	4
2	3		0	8	11	2
3	6	1		6	13	1
4	5	4	3		12	3
Losses	14	5	7	17	43	Total

Cage II

Rat no.	1	2	3	4	Wins	Rank order
1		3	1	4	8	3
2	5		3	0	8	2
3	0	0		1	1	4
4	4	7	3		14	1
Losses	9	10	7	5	31	Total

Rat no.	1	2	3	4	Wins	Rank order
1		9	1	11	21	1
2	4		0	10	14	3
3	0	2		2	4	2
4	7	4	0		11	4
Losses	11	15	1	23	50	Total

Cage III

Rat no.	1	2	3	4	Wins	Rank order
1		7	5	14	26	2
2	7		4	10	21	1
3	2	0		1	3	4
4	9	0	1		10	3
Losses	18	7	10	25	60	Total

Rat no.	1	2	3	4	Wins	Rank order
1		0	1	0	1	3
2	5		3	22	30	1
3	0	0		3	3	1
4	0	1	1		2	4
Losses	5	1	5	25	36	Total

Cage IV

1st period

Rat no.	1	2	3	4	Wins	Rank order
1		2	9	6	17	1
2	1		5	6	12	3
3	1	2		10	13	4
4	11	9	2		22	2
Losses	13	13	16	22	64	Total

2nd period

Rat no.	1	2	3	4	Wins	Rank order
1		6	3	7	16	1
2	2		5	5	12	4
3	1	4		9	14	2
4	3	7	6		16	3
Losses	6	17	14	21	58	Total

Cage V

Rat no.	1	2	3	4	Wins	Rank order
1		1	0	0	1	4
2	0		5	4	9	3
3	0	13		4	17	2
4	1	9	6		16	1
Losses	1	23	11	8	43	Total

Rat no.	1	2	3	4	Wins	Rank order
1		1	0	5	6	Mixed
2	2		6	11	19	
3	2	9		8	19	
4	0	7	11		18	
Losses	4	17	17	24	62	Total

Cage VI

Rat no.	1	2	3	4	Wins	Rank order
1		1	4	1	6	4
2	1		2	0	3	2
3	4	2		0	6	3
4	9	1	3		13	1
Losses	14	4	9	1	28	Total

Rat no.	1	2	3	4	Wins	Rank order
1		1		3	4	4
2	3		5	13	21	2
3	0	4		1	5	3
4	5	24	7		36	1
Losses	8	29	12	17	66	Total

Test 12

Rat no.	1	2	3	4	Wins	Rank order
1		10	4	22	36	2
2	8		1	13	22	4
3	9	4		7	20	1
4	10	22	0		32	3
Losses	27	36	5	42	110	Total

Cage I

Rat no.	1	2	3	4	Wins	Rank order
1		9	0	12	21	2
2	3		0	10	13	3
3	1	3		1	5	1
4	9	6	0		15	4
Losses	13	18	0	23	54	Total

Cage II

1st period

Rat no.	1	2	3	4	Wins	Rank order
1		7	8	12	27	1
2	1		6	6	13	4
3	2	8		6	16	2
4	9	8	1		18	3
Losses	12	23	15	24	74	Total

2nd period

Rat no.	1	2	3	4	Wins	Rank order
1		13	14	26	53	1
2	0		0	1	1	4
3	5	0		5	10	2
4	7	0	5		12	3
Losses	12	13	19	32	76	Total

Cage III

Rat no.	1	2	3	4	Wins	Rank order
1		7	19	8	34	1
2	0		0	0	0	4
3	19	3		8	30	3
4	2	5	10		17	2
Losses	21	15	29	16	81	Total

Rat no.	1	2	3	4	Wins	Rank order
1		1	1	6	8	2
2	0		0	1	1	4
3	1	1		0	2	3
4	6	15	5		26	1
Losses	7	17	6	7	37	Total

Cage IV

Rat no.	1	2	3	4	Wins	Rank order
1		14	6	10	30	1
2	13		10	3	26	2
3	5	3		5	13	3
4	6	1	3		10	4
Losses	24	18	19	18	79	Total

Rat no.	1	2	3	4	Wins	Rank order
1		5	1	15	21	1
2	2		0	0	2	4
3	0	0		5	5	2
4	4	4	0		8	3
Losses	6	9	1	20	36	Total

determining the final result were operating contemporaneously between the rats, each position can be assessed separately without reference to the ultimate characteristic of any other position, by expansion of the binomial $(\frac{1}{4} + \frac{3}{4})^{12}$. We then find that the likelihood that position 1 would be stable in 7 out of 12 cases would be expected, if random movements were present, to occur less than 1 in 100 times ($P<0{\cdot}01$) and the constancy of the lowest ranking rat to occur in less than half a million times ($P<0{\cdot}000002$). The constancy shown by the position of these two rats, therefore, is in itself evidence of stable elements in the order of rank within the group.

Again, where a change-over in position between two animals takes place these animals are often in the first instance very close. For example in cage 1 of the males in the first three weeks Rat 1 beat Rat 3 ten times and lost to him nine times, but in the second three weeks, Rat 3 beat Rat 1 eighteen times out of twenty encounters.

A second point shown by these results is the remarkable drop in the number of encounters in the second period of the tests done in normal lighting conditions. This drop is, on the average, about 50 per cent. In reversed lighting conditions this drop, though still apparent, is not nearly so marked; this may be due to the shorter time intervals concerned.

The results with female rats (Table IV) show

that the constancy over the two periods is very much less than that shown by the males. It is still a little more constant than we would expect by purely random movements.

From our observations it is clear that the oestrous behaviour on the part of any single animal seriously alters the pattern of social interaction and may thus affect the rank order. Thus, on the day when a female is in heat she is liable to be chased and pounced on by all the other females in the cage, the stimulus for these attacks being her own behaviour of running away and posturing.

All the female groups shown here were observed under reversed lighting conditions, as under normal conditions the incidence of encounters was so low as to make any sort of ranking impossible. These results should then be compared with the last three cages of males (Table III). One very noticeable difference is the small number of resolved encounters observed, only a little more than 25 per cent. of the number observed in the males.

Rank Order and Socio-Sexual Encounters

In this study, since mounting behaviour was a frequent and obvious accompanying activity of all social encounters, details of its occurrence and direction were recorded in the males. The correlation between this behaviour and rank order is by no means simple. If, however, the animals are placed in order of rank and the number of mounts attributable to each rank as well as the number of mounts directed at that rank by other rats is noted, the following summary (Table V) of 12 cages of 4 males is obtained.

Table V. Summary of Relation Between Rank Order and Socio-sexual Behaviour in Male Rats

Rank position	No. of times mounting	No. of times mounted
1	64	113
2	51	99
3	102	43
4	97	59
x^2	$<0{\cdot}02$	$<0{\cdot}001$

This suggests that the social attention of the subordinate rats is to some extent directed towards the higher ranks (see third column of Table V). It is also seen that the rats lower in the order are more active in this behaviour.

Discussion

We are aware, that, although the results obtained by using this particular metameter—the full submissive posture—have enabled us to define rank order adequately, we could in the appropriate circumstances, using a full analysis of the agonistic behaviour, get a much more sensitive method of distinguishing the rank of each rat. It is important to appreciate, however, that we have chosen a single metameter, and this one in particular, because it is the most clear-cut evidence of the resolution that takes place in encounters between rats. It will, therefore, be present in most, if not all circumstances, whereas other elements are part of a more malleable pattern. This is well seen from the fact that in cages in which low-level play is predominant there is little difference between the rat lowest in rank and the others in the group, whereas when an intruder is present it is easy to distinguish the rat lowest in rank, as his behaviour is then quite distinct. The lowest rat of a cage of 4 retired from the social scene to a position under the food hopper for most of the time the intruder was settling in. A noticeable, but less marked, differentiation of the behaviour of the other rats also appears. This brings out the value of a single metameter which is unaffected by differences in the environment.

The behaviour of rats in groups that we have been studying is essentially playful, as the level of activity in undisturbed cages is very low in comparison with that in conditions which stimulate fighting. However, comparison of this behaviour with that of fighting seen, for example, when a strange male is introduced into an established group of males, shows the essential identity of the various postures we have used with those seen in true fighting. These postures in either sex are essentially similar to those seen by Seward (1945). Seward (1945) in his description of the fighting behaviour refers to these postures without much detailed description and, as they are given a meaning without any logical framework with which to assess the validity of his interpretation, we cannot usefully relate our findings to what is, in effect, the only comparable study.

Seward kept his rats in separate cages and fought them in pairs in a neutral cage. Using this technique he was unable to get any stability in the ranking of his rats. We feel that this lack of pattern is due to the lack of social contact between the rats, our ranking being due to constant interaction between all rats in the group. For

example, one of the more common ways of release of tension in fighting is a re-directional activity down the order, e.g. A & B are fighting and B breaks away and beats C, an animal lower in rank than either A or B. This sort of thing, of course, cannot happen in staged pair fights.

On one or two specific points about the fighting we are in agreement with Seward (1945). He found a marked decrease in the number of agonistic encounters as the male rats aged, this being apparently a quite sudden decrease shortly after puberty along with, as in our case, an increase in intensity of these encounters. He also found that with females what little pattern he did get was no longer shown and also the frequency of fighting was very much lower; this again is in agreement with our own results.

It is our intention to obtain an inherent framework of reference to interpret the relationships of the various components of conflict behaviour. As, moreover, we have revealed a relationship between position in rank and another aspect of social behaviour, e.g. a component of sexual behaviour, the interpretation will have to be part of a wider framework relating all aspects of social activity.

The number of times the high ranking rats were mounted provides evidence that the subordinate males of a hierarchy are attracted to those holding more dominant status. It is interesting to note that this feature was postulated as the basis for the sociability of monkeys (Chance, 1955).

Summary

1. A method is described whereby rank order may be determined in cages containing rats of either sex by simple observation of their behaviour in the cage.

2. Rank order was found to develop in cages containing 2, 3, 4 and 5 male rats but not in cages containing 6 male rats when assessed during the first three weeks after weaning.

3. Males develop linear orders which are stable or tend to intensify with time during nine weeks following weaning. Females show the same feature but to a less marked degree.

4. The lowest in rank of the males is the most constant in position.

5. The sexual (mounting) behaviour of different individuals has been assessed in relation to their position in the hierarchy. The dominant rats are more frequently mounted.

6. The positions 1 and 4 of the males in cages of 4 have been tested for stability by a simple statistical method and provide confirmatory evidence that the groups possess a stable structure.

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THE BEHAVIOUR OF THE MULTIMAMMATE MOUSE, *Rattus (Mastomys) natalensis* (A. Smith)

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Introduction

For the past nine years a colony of Mastomys has been maintained by Mr. D. H. S. Davis at this Institute, and during this time the usefulness of this species has been investigated in many different fields of medical research. Mastomys is extremely susceptible to *Pasturella pestis*, (Davis & Murray, 1956) and is now used for routine plague testing. It has also been shown to be very susceptible to bilharziasis (*Bilharzia mansoni*) and has proved a most suitable species for experiments with this parasite (Lurie & de Meillon, 1956). In captivity this species furthermore develops spontaneous adenocarcinoma of the glandular stomach with extraordinary frequency (Oettlé, 1955)—a remarkable fact since carcinoma of the glandular stomach is exceedingly rare in all other animal species investigated (Stewart, 1953), while representing one of the commonest cancers in man. The present studies were undertaken as part of an investigation of stomach cancer susceptibility, in the hope that a better understanding of the behaviour of this rodent would help in its management in captivity and possibly also its control in the field, for Mastomys is an important vector of plague in South Africa.

Description

In appearance Mastomys is intermediate between a rat and a mouse, (Plate IIIA). Its weight rarely exceeds a hundred grams. The hair is moderately long and fine, and the coat colour in the wild type is slate in the young, becoming agouti when mature and a more drab agouti when old. In Davis' colony a recessive dilute agouti strain has emerged with a paler coat colour and red eyes as distinct from the dark agouti coat and black eyes of the wild type.

Habits in the Field

Mastomys is found over the entire continent of Africa (Shortridge, 1934). In this wide climatic and geographic range it has adapted itself to different habitats but is found mainly in dense bush and cultivated areas. Only in arid mountains and plains are they rare. Mastomys abounds in outhouses and native huts as well as in lofts, for they are fair climbers (Plate III B and C). They are semi-domestic and take the place of the house mouse in rural districts. Their migratory habits make them an important link between domestic rats and the wild rodent reservoir of plague in South Africa.

Mastomys uses the deserted burrows of other animals wherever possible. If forced, it will burrow, but only where the soil is soft or cracked (Davis, 1955). Although Mastomys uses outhouses as a refuge, nesting is usually underground. Several families live in one burrow and when food is plentiful they increase rapidly, being prolific breeders (Oliff, 1953). In certain seasons Mastomys populations show enormous increases. This is due to a higher survival rate of the young, probably because of a more abundant food supply usually after heavy rains. Such population increases of Mastomys have occurred on several occasions in Zululand during the past twenty-five years and favour the spread of plague (Davis, 1946, 1948).

While food is plentiful Mastomys is found in daily association with other rodents (Rattus, Tatera, Mus and Rhabdomys) but when competition leads to food scarcity, Mastomys gives way. It appears to be driven away from habitations where Rattus has established itself in large numbers, and does not occur in large towns (Shortridge, 1934). Mastomys is omnivorous though mainly granivorous. It will travel several miles when food is scarce. Spasmodic hoarding takes place, possibly as they prefer to eat at the nest site. In winter, nevertheless, Mastomys still is obliged to forage.

General Behaviour in the Laboratory

In the laboratory the behaviour of Mastomys is compatible with its field habits, being nervous, quick to escape and conscious of danger, and consequently it is difficult to handle and often bites without provocation. It is very tolerant of rodent neighbours, both of its own and of other species. Mixed or unisexual groups live together without fighting apart from ear nibbling or scuffling. Belligerence is absent even during

breeding periods. Mated animals have remarkably clean habits and attempt to dispose of refuse by depositing through any available hole in the cage. Burrows occupied by Mastomys rarely contain droppings (Schultz, 1951). Cages containing animals of one sex only, however, are usually dirty.

Materials and Methods

Animals

For activity experiments, two mature wild-type males, distinguished here as A and B, were selected from the laboratory bred stocks, together with one recent captive. Observations were also made on several families and individuals, laboratory-bred (wild-type and dilute) and recent captives. The laboratory-bred animals were about 200 days old; wild-type captured animals have been shown to be under the age of one year for the most part.

Activity Studies

The activity cage (see Appendix) was of wire gauze across which a beam of light passed and was received on a photoelectric cell which marked a smoked drum when the beam was interrupted. Food and water were placed at one end of the cage and were in continuous supply. At the other end of the cage a glass jar (diameter 2″) painted black was provided as a retreat.

The cage was kept in a cupboard near a north-facing window. The cupboard door was closed when continuous darkness was required, and also when continuous illumination was obtained from an electric lamp. Temperature was thermostatically controlled at $70° \pm 5°$F.

Observation

An observation cage was constructed with sides and back of frosted glass and the front interchangeably transparent plate glass or dark neutral tint plate (80 per cent. absorption) to act as a one way screen when the cage was illuminated from within. The dimensions of this cage are 22″ x 18″ x 3″ from front to back. The latter dimension represents the depth of field of a camera lens at f.11 and a magnification of 0·1 x (Morgan & Lester, 1951).

Results

Activity has been recorded as counts per hour representing the number of times the animal crossed the light beam. The results are summarised in Tables I-VI and Figs. 1 to 4.

Discussion

Both the recent captive (Table I, Fig. 1) and the laboratory bred (Table II, Fig. 1 and 4) animals show a 24-hour activity cycle with a marked increase at night. The recent captive animal shows two peaks of activity, one at dusk and a larger one at sunrise. The laboratory bred animal shows only the latter peak. Twenty-eight per cent. of the total activity of the laboratory bred animal is exhibited during the day whereas this figure is 12·7 per cent. for the recent captive. The results suggest that the recent captive has the stronger innate cycle. The difference in the laboratory bred animals may possibly be the result of regular daily disturbances in the animal-house.

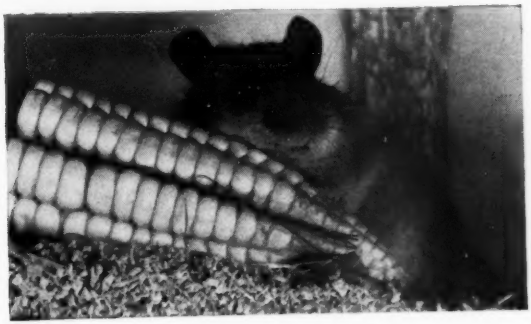
1. Although both animals were allowed one week in the cages before the experiments began, the recent captive was slower to become accustomed to cage surroundings. This is shown by an increase in the total daily count which was not demonstrated by the laboratory bred animal (Tables I and II). When introduced into the cage the laboratory bred animal at once began to reconnoitre while the recent captive remained motionless in a far corner for well over four hours.

2. In continuous artificial light and to a greater extent in total darkness, the laboratory bred animal (A) showed a peculiar disturbance of its daily rhythm. In continuous artificial light (Table VI) alternate periods of high and low activity persisted but the timing was upset, the period of low activity commencing later each day, the length of the low activity period being unrelated to that of high activity.

In total darkness (Tables IVa, IVb and Fig. 2), the animal showed a similar disturbance of timing but the period of low activity was nearly equal in length to that of high activity. The second laboratory bred animal (B) also showed an upset rhythm in total darkness (Table IVc). The period of low activity was equal to or less than the period of high activity in hours per day. The peak of activity varies in magnitude and time of occurrence, variation being from 32 to 105 counts per hour from 6-7 a.m. to 12-1 p.m. The fluctuation in peak activity appeared to be a random change.

In the recent captive, in continuous darkness, the active period began earlier and continued longer, but the peaks were still at night although they occurred some hours earlier. Apart from this there was no progressive shift in the timing of the cycle.

PLATE III



A. Mastomys, male, wild-type

B. Mastomys climbing

C. Mastomys climbing

D. Male bullying oestrus female

Table I. Mastomys Male, Wild Type, Recent Captive: Activity in Counts per Hour. Cage exposed to North Window.

	October						Average
	*25–26	*26–27	27–28	*28–29	*29–30	30–31	
12–1 p.m.	0	0	0	0	0	0	0·00
1–2	0	0	0	0	0	0	0·00
2–3	0	0	0	1	0	0	0·17
3–4	0	1	2	3	0	0	1·00
4–5	3	2	3	2	0	0	1·67
5–6	9	4	0	0	0	0	2·17
6–7	4	6	8	0	0	0	3·00
7–8	2	2	1	20	14	16	9·17
8–9	7	6	2	18	13	17	10·50
9–10	6	2	8	11	14	7	8·00
10–11	5	7	2	9	2	22	7·83
11–12 midnight	0	2	2	18	5	9	6·00
12–1 a.m.	0	2	2	16	4	7	5·17
1–2	4	6	4	8	13	22	6·17
2–3	5	3	2	0	0	16	4·33
3–4	6	15	9	14	4	15	10·50
4–5	13	5	10	21	13	14	12·56
5–6	5	9	16	21	15	28	15·67
6–7	2	0	2	12	6	8	5·00
7–8	3	0	4	2	4	0	2·17
8–9	0	0	0	0	0	0	0·00
9–10	0	0	0	0	0	6	1·00
10–11	0	0	0	6	0	0	1·00
11–12 noon	0	0	0	0	0	1	0·17
Total	74	72	77	182	107	168	113·36
Average number of counts from 6 a.m.–6 p.m.							14·35
Average number of counts from 6 p.m.–6 a.m.							99·01
Average percentage activity during the day							12·65%
Average percentage activity during the night							87·35%

*Day cloudy to dull.

In continuous light the peak at sunrise was retained, the period of activity was extended into the day once more, and once again there was no progressive change in the timing.

3. As the animal always kept a supply of food in its nest, feeding was not invariably recorded.

4. The disadvantages of the apparatus used are:

(*a*) A visible beam might possibly interfere with behaviour and during experiments in continuous darkness animals frequently sat for periods up to three minutes in the light beam.

(*b*) Analysis of different types of movements was not possible

(*c*) Small movements such as washing or eating are not recorded, so that the results do not portray the precise alternation of sleep and wakefulness.

An improved cage for absolute readings has been described by Albino (1951) where the cage movements themselves are recorded by a counter and a kymograph. This might be combined with a series of infra-red beams to record different types of movements, e.g. at the nest or food tray.

General Activities

Feeding

Mastomys prefers hard foods such as grains. These, irrespective of their size, are usually held in the fore paws, but only the smaller foodstuffs are lifted to the mouth.

Drinking

Drinking is by lapping except in the very young, which suck.

Locomotion

Outside the cage Mastomys usually escapes by a hop-and-jump gait. Once out of immediate danger this is usually followed by a purposive run. The body is very low slung and the tail is stiffened. In strange terrain, when undisturbed, the animal proceeds very slowly at first, using a slinking belly-crawl, with feet splayed out while

Table II. Mastomys Male, Wild Type, Laboratory Bred (A): Activity in Counts per Hour. Cage exposed to North Window

	October						
	*25–26	*26–27	*27–28	*28–29	*29–30	30*31	Average
12–1 p.m.	0	0	0	0	0	0	0·00
1–2	0	0	0	11	16	0	4·50
2–3	7	0	0	2	0	3	2·00
3–4	24	1	6	0	0	0	5·17
4–5	9	4	0	0	2	8	3·83
5–6	30	0	0	0	0	0	5·00
6–7	21	4	16	0	0	14	9·17
7–8	19	3	1	0	0	8	5·17
8–9	16	9	4	0	0	6	5·83
9–10	32	12	3	29	16	25	17·83
10–11	41	24	3	0	15	14	16·17
11–12 midnight	48	41	50	24	14	9	31·00
12–1 a.m.	40	49	35	46	5	7	30·33
1–2	54	70	66	44	37	40	51·67
2–3	77	88	80	79	68	86	79·67
3–4	75	85	95	63	57	54	71·50
4–5	64	92	119	62	74	84	83·33
5–6	101	72	104	76	69	90	85·33
6–7	43	70	113	84	52	103	80·83
7–8	25	11	136	30	100	50	58·67
8–9	24	2	30	19	35	26	22·67
9–10	28	0	0	0	0	4	5·33
10–11	0	1	6	0	0	0	1·17
11–12 noon	0	0	0	0	0	1	0·17
Total	778	638	867	569	560	632	676·34
Average number of counts from 6 a.m.–6 p.m.	..	..	..	..	..	..	189·34
Average number of counts from 6 p.m.–6 a.m.	..	..	..	..	..	..	487·00
Average percentage activity during the day	..	..	..	..	..	..	27·99%
Average percentage activity during the night	..	..	..	..	..	..	72·01%

*Day cloudy to dull.

it sniffs repeatedly. In directive walking Masttomys rarely, if ever, retraces its steps. It is a fair climber (Plate III B and C), and can also exhibit surprising jumps (up to 18″) especially when escaping.

Swimming

In water, Mastomys shows very little fear and floats easily, first looking from side to side and sniffing until it begins to swim but following a definite direction. The mode of swimming follows the familiar dog-paddle and is fairly effective.

Washing

Immediately on waking, the eyes are thoroughly cleaned by alternately licking the paws and wiping the eyes. Sometimes the closed eye is scratched with very rapid movements of a rear paw: here again the paw is licked after each bout of scratching. After eating or drinking the wash is usually confined to the head region and is not extensive.

The drying wash after submersion is far more extensive and thorough, the paws rubbing over the muzzle and eyes, and the moisture is then licked off. If the paws are very wet they are shaken dry by very rapid vibrations. The body is next licked dry. The flanks are reached by sitting on the haunches with the forepaws on the knees and the licking accomplished with an up and down movement of the head. The rear limbs are reached by squatting on alternate haunches, the limb receiving attention being held with the forepaws. To retain balance in this position Mastomys leans against any available object.

Washing also appears to be a definite displacement action in younger animals. When placed on a strange terrain the first action after a brief sniff is to wash; this wash is of limited extent and brief duration. Washing is also exhibited as a displacement activity when the escape drive is thwarted, e.g. if an animal, on a small plank floating on water, is subjected to a pinch on the tail. In older animals, washing, as a displacement activity, is replaced by aimless

Table III. Mastomys Male. Wild Type, Recent Captive: Activity in Counts per Hour. Cage in continuous darkness.

	December				
	2–3	3–4	4–5	5–6	Average
12–1 p.m.	6	1	6	2	3·75
1–2	0	3	0	4	1·75
2–3	7	2	9	2	5·00
3–4	0	34	20	2	14·00
4–5	6	40	41	13	25·00
5–6	33	4	46	38	30·25
6–7	6	23	7	19	13·75
7–8	13	2	19	16	12·50
8–9	22	24	12	17	18·75
9–10	25	37	27	19	27·00
10–11	23	17	9	27	19·00
11–12 midnight	24	19	41	13	24·25
12–1 a.m.	36	29	2	14	20·25
1–2	35	25	36	13	27·25
2–3	56	40	22	13	32·75
3–4	53	17	25	5	25·00
4–5	31	4	20	30	21·25
5–6	21	4	6	19	12·50
6–7	0	0	14	0	3·50
7–8	12	14	2	7	8·75
8–9	11	8	17	4	10·00
9–10	3	5	2	14	6·00
10–11	1	2	4	4	2·75
11–12 noon	6	6	0	6	3·25
Total	430	360	387	301	368·25
Average number of counts from 6 a.m.–6 p.m.	..	..	..	..	114·00
Average number of counts from 6 p.m.–6 a.m.	..	..	..	..	254·25
Average percentage activity during the day	..	..	..	..	30·13%
Average percentage activity during the night	..	..	..	..	69·87%

running confined to a small space, and accompanied by much sniffing. Disturbance of the nest, for example, is followed by washing if the parents are young or by aimless running if the parents are old.

Individuals do not groom one another except in the case of females in or near oestrus which are "groomed" by males—this activity seems more in the nature of "bullying" as it is rough and sometimes accompanied by nibbling: the female submits passively (Plate III D).

Burrowing

Recent captives, when placed in a vivarium containing loose moist sand, will dig holes but for the first two days and thereafter form tunnels in which they shelter. A plaster cast of the burrow from the vivarium shows an intricate interleading system of tunnels without apparent order or central chamber.

Digging is accomplished "terrier" fashion, mainly by the female. This activity can be induced by sprinkling water on the surface to simulate rain. Laboratory bred animals introduced into the same cage remain on the surface and join the recent captives in the burrow only when danger threatens. After a few days they also begin to dig but do not make a hole sufficiently large to hide in. After two weeks they too remain in the burrow and dig new side tunnels.

It seems that although burrowing is an innate activity, proficiency requires experience. The fact that whenever possible Mastomys uses deserted burrows and never digs in hard soil suggests that it probably is not a competent burrower.

Antagonistic Behaviour

To the sight and smell of man the recent captive shows a great amount of escape reaction. The laboratory bred male, on the other hand, frequently adopts a defence stance on its haunches, uttering a rough medium-pitched screech. In this position one may touch the neck or stomach region without fear of a bite; the animal remains on its haunches and continues screeching without retaliatory movements, although if the muzzle be touched from below, a bite will certainly ensue. Eventually it will come

Table IVa. Mastomys Male. Wild Type, Laboratory Bred (A): Activity in Counts per Hour. Cage in continuous Darkness

	November				
	10–11	11–12	12–13	13–14	Average
12–1 p.m.	50	71	51	25	49·25
1–2	55	57	54	37	50·75
2–3	46	83	56	17	50·50
3–4	120	115	39	25	74·75
4–5	71	155	47	15	72·00
5–6	32	112	49	24	54·25
6–7	4	73	56	27	40·00
7–8	0	33	62	37	33·00
8–9	0	4	74	47	31·25
9–10	22	3	18	25	17·00
10–11	0	4	0	62	16·50
11–12 midnight	0	0	8	83	22·75
12–1 a.m.	0	2	0	13	3·75
1–2	0	0	6	8	3·50
2–3	0	4	0	0	1·00
3–4	1	0	4	5	2·50
4–5	6	0	0	0	1·50
5–6	0	4	7	2	3·25
6–7	4	0	3	7	3·50
7–8	17	9	0	0	6·50
8–9	15	0	3	0	4·50
9–10	41	20	0	5	16·50
10–11	66	33	2	2	25·75
11–12 noon	78	54	2	11	36·25
Total	628	836	541	477	620·50
Average number of counts from 6 a.m.–6 p.m.					444·50
Average number of counts from 6 p.m.–6 a.m.					176·00
Average percentage activity during the day					71·64%
Average percentage activity during the night					28·36%

down on its forepaws and attempt to escape. If one blows a stream of air at the animal while handling it, however, it will remain on its haunches, screeching without any attempt to escape.

When handled, or even as soon as the cage lid is removed, many animals attack with a quick snap followed by an immediate attempt to escape. Less frequently the bite is prolonged and deep and the animal does not release its grip. The particular conditions inducing this second type of biting have not yet been classified.

Towards other rodents, including those of its own species, Mastomys is non-aggressive and cannot be induced to fight whatever the succession or sex of the animals introduced, even when females are in oestrus. This suggests that the territorial instinct, at best, is very weak. Frequent scuffles and tugs-of-war may, however, take place over food. These are not serious, last but a moment and induce no retaliation. Certain males are inclined to nibble the ears of their companions, who suffer in silence and without apparent resentment. Cannibalism occurs and dead or dying animals are often eaten by their cage mates, which invariably start at the head, the eyes as a rule, being eaten first.

With a caged pair the male undertakes all the guarding, and sits at the entrance biting at any object that threatens. The female will attack only if the danger threatens the litter. The ferocity of the female lessens with successive litters. In danger (e.g. when teased with a piece of rubber tubing) the defensive male chatters its teeth, then squeaks, closes its eyes, and bites. Once the tubing has been bitten, and is motionless, it is ejected from the cage. If this occurs in the vicinity of the nest the female usually transfers the whole nest and young to the other side of the cage.

A peculiar defensive action is seen in a rapid movement of the forepaws in the direction of the danger; handy objects, such as food cubes, are also pushed in the direction from which the threat comes. This movement is identical with that shown by animals closing the entrance to their burrows from within. It is also displayed in killing an insect such as a cockroach.

Table IVb. Mastomys Male. Wild-type, Laboratory Bred (A): Activity in Counts per Hour. Cage in Continuous Darkness

	Cage exposed to North window		Cage in continuous darkness									Cage exposed to North window		
	December													
	7–8	8–9	9–11	10–11	11–12	12–13	13–14	14–15	15–16	16–17	17–18	18–19	19–20	20–21
12–1 p.m.	0	2	1	3	54	87	69	59	46	1	1	0	11	0
1–2	1	0	0	2	56	113	84	73	52	8	0	0	3	0
2–3	0	0	0	0	31	101	73	78	44	25	6	0	1	0
3–4	0	0	3	0	4	90	88	94	79	28	22	1	2	7
4–5	2	0	2	0	0	51	120	93	76	43	35	0	4	0
5–6	5	10	1	1	0	31	98	111	84	25	69	0	0	8
6–7	11	5	0	2	3	14	24	95	76	79	52	4	0	11
7–8	2	7	10	0	3	0	9	41	73	72	68	28	1	0
8–9	5	1	4	0	0	0	4	28	41	83	74	35	4	3
9–10	28	16	3	3	3	0	6	21	28	49	101	32	23	33
10–11	39	20	4	0	4	0	11	10	21	116	103	42	29	21
11–12 midnight	43	39	36	4	4	0	10	4	14	56	54	54	19	17
12–1 a.m.	44	53	43	3	3	0	5	6	10	38	23	81	46	24
1–2	56	51	43	23	0	0	11	3	11	3	18	96	53	54
2–3	54	63	59	38	5	1	2	10	16	3	12	48	59	67
3–4	91	77	55	56	17	0	2	0	13	4	3	73	84	84
4–5	90	79	86	54	15	5	2	0	8	0	2	101	67	96
5–6	103	98	118	46	33	4	3	5	3	1	1	43	75	99
6–7	41	53	56	59	78	14	14	15	2	0	2	18	104	116
7–8	20	48	68	96	69	12	18	0	2	0	5	4	78	95
8–9	18	23	73	87	55	32	10	6	8	1	8	4	32	53
9–10	1	0	44	99	86	20	8	10	0	5	0	8	4	4
10–11	0	0	29	110	80	43	33	14	0	11	0	0	0	0
11–12 noon	1	0	8	81	98	66	36	19	2	2	0	0	0	1
Total	655	646	746	767	701	684	740	795	710	653	659	671	699	793

Table IVc. Mastomys Male, Wild-type, Laboratory Bred (B). Activity in Counts per Hour. Cage Exposed to North Window, and in Continuous Darkness.

	Cage exposed to North window						Cage in continuous darkness									
	May						June									
	30–31	31–1	1–2	2–3	3–4	Average	4–5	5–6	6–7	7–8	8–9	9–10	10–11	11–12	12–13	13–14
12–1 a.m	2	0	0	8	10	4·00	4	6	20	0	5	11	2	14	8	105
1–2	0	0	1	2	0	1·20	3	13	8	36	27	2	12	21	0	17
2–3	2	0	0	0	4	2·40	0	0	0	0	9	1	0	7	12	19
3–4	0	0	0	0	0	0·00	1	6	3	0	5	3	5	0	0	6
4–5	1	0	0	0	0	0·40	1	6	3	0	5	6	0	4	0	3
5–6	0	0	0	0	0	0·00	1	8	3	0	2	4	6	0	0	3
6–7	0	7	5	5	6	4·60	0	15	0	0	2	0	0	0	6	0
7–8	6	0	0	0	0	1·20	2	0	3	0	3	0	0	0	0	5
8–9	7	0	2	0	2	2·20	4	7	3	0	0	6	6	3	1	1
9–10	10	2	0	9	1	4·40	2	3	14	6	2	0	0	0	3	2
10–11	10	0	3	4	0	3·40	9	9	4	0	2	3	2	2	7	6
11–12	32	2	15	10	7	13·20	6	2	13	2	7	4	6	10	5	2
12–1	34	22	9	12	0	15·40	11	12	49	14	6	5	2	6	29	13
1–2	22	17	16	17	4	15·20	10	10	15	3	4	8	15	0	25	18
2–3	21	15	15	21	7	15·80	15	13	26	22	41	15	10	12	32	20
3–4	26	11	7	20	27	20·20	14	20	21	14	35	13	15	7	26	8
4–5	31	24	22	21	3	20·20	33	19	25	20	39	45	19	12	37	23
5–6	62	30	19	19	14	28·80	19	28	24	30	46	18	26	29	16	50
6–7	41	24	19	15	18	23·40	32	20	30	37	40	53	32	7	25	51
7–8	69	58	42	19	17	41·00	18	28	69	53	29	45	33	40	12	49
8–9	12	21	42	59	43	35·40	10	34	84	67	51	67	48	42	29	60
9–10	4	6	10	34	24	15·60	26	11	19	101	145	59	54	48	31	61
10–11	0	26	3	2	11	8·40	5	6	0	78	149	84	36	46	24	24
11–12	6	0	0	4	3	2·60	2	5	6	7	0	51	4	11	57	16
Total	398	265	240	281	201	277·00	227	277	439	483	652	503	333	321	385	562

Table V. Mastomys Male. Wild-type, Recent Captive: Activity in Counts per Hour. Cage in continuous artificial light.

	November 22–23	23–24	24–25	25–26	Average
12–1 p.m.	8	29	10	11	14·50
1–2	24	13	0	7	11·00
2–3	6	1	17	10	8·50
3–4	18	14	1	3	9·00
4–5	1	5	11	9	6·50
5–6	0	0	1	0	0·25
6–7	46	19	0	0	16·25
7–8	22	17	13	20	18·00
8–9	10	4	3	10	6·75
9–10	15	12	2	4	8·25
10–11	2	12	38	30	20·50
11–12 midnight	40	22	6	33	25·25
12–1 a.m.	42	22	9	26	24·75
1–2	59	14	6	14	23·25
2–3	57	5	9	10	20·25
3–4	58	4	46	26	33·50
4–5	45	34	33	42	38·50
5–6	57	47	40	44	47·00
6–7	33	26	12	39	27·50
7–8	26	28	33	37	31·00
8–9	48	38	42	41	42·25
9–10	38	31	58	36	40·75
10–11	13	17	35	24	22·25
11–12 noon	1	15	6	12	8·50
Total	669	429	431	488	504·25
Average number of counts from 6 a.m.–6 p.m.					222·00
Average number of counts from 6 p.m.–6 a.m.					282·25
Average percentage activity during the day					44·03%
Average percentage activity during the night					55·97%

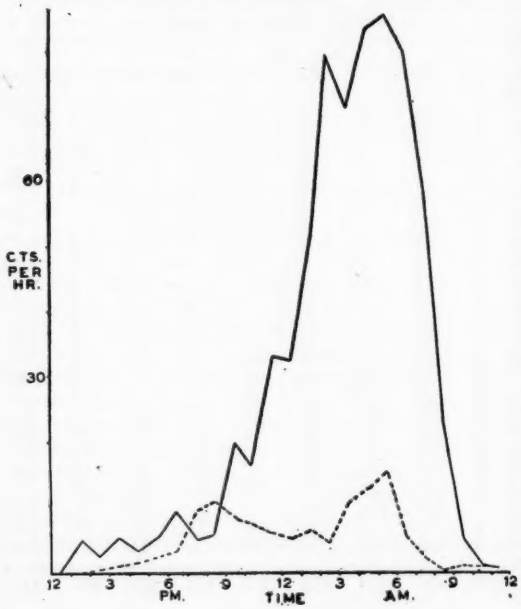


Fig. 1. Comparison of the activity curves of the recent captive (dotted line) and the laboratory bred animal (A) (unbroken line). Cages exposed to north window. Tables I and II.

Mastomys appears to be very subject to stress and on one occasion a female died when a dog sniffed at her cage. A post-mortem examination revealed extreme dilation of both ventricles of the heart, presumably indicating acute cardiac failure.

Mating

The male is always allowed near the female but is only permitted to mount at oestrus. If the male attempts to do so before, he is rejected by a kick from a hind paw. Copulation has not been observed during the day and it seems that the female comes on heat only at night. Several females were injected with estradiol benzoate in an attempt to induce oestrus behaviour during daylight. Although the males did not mount they were evidently excited and spent much time in digging and nibbling the sawdust. As the effects of the oestrogen on the female disappeared, the males stopped these activities which possibly represent further forms of displacement.

Table VI. Mastomys Male. Wild-type, Laboratory Bred (A): Activity in Counts per Hour. Cage in continuous Artificial Light

	November 14–15	15–16	16–17	17–18	Average
12–1 p.m.	33	44	24	0	25·25
1–2	48	35	25	0	27·00
2–3	66	24	3	6	24·75
3–4	55	68	25	19	41·75
4–5	30	47	30	17	31·35
5–6	75	49	32	30	45·00
6–7	74	83	12	35	51·00
7–8	110	49	30	25	53·50
8–9	68	64	39	25	49·00
9–10	5	26	35	19	21·25
10–11	0	6	39	33	19·50
11–12 midnight	1	4	42	21	17·00
12–1 a.m.	8	0	25	17	12·50
1–2	0	7	14	19	10·00
2–3	0	0	12	0	3·00
3–4	9	0	6	0	3·75
4–5	0	2	10	3	3·75
5–6	5	0	14	2	5·25
6–7	0	0	8	0	2·00
7–8	0	0	2	0	0·50
8–9	0	0	0	0	0·00
9–10	0	0	0	2	0·50
10–11	7	4	11	13	3·25
11–12 noon	0	0	2	0	0·50
Total	594	512	430	274	451·25
Average number of counts from 6 a.m.–6 p.m.					201·75
Average number of counts from 6 p.m.–6 a.m.					249·50
Average percentage activity during the day					44·71%
Average percentage activity during the night					55·29%

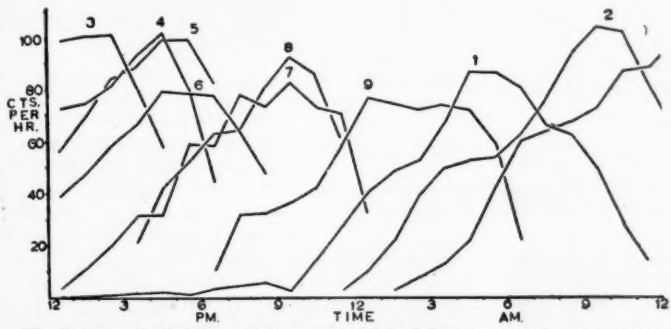


Fig. 2. Smoothed daily activity curves of the laboratory bred animal (A). Continuous darkness. Table 4b. (1) 9th—10th December. (9) 18th—19th December.

Nesting

The nesting material is not shredded unless it does not otherwise permit construction of a nest. Shortly before parturition nest building is greatly accelerated. These nests undergo much alteration and the female constantly increases the nest size if material is available. The tendency is always to construct upwards rather than spreading and if the material allows (tissue paper or a mealie leaf) the female will stand in the middle of the floor of the nest, depositing the material in a circle around her, mainly using the muzzle. The female ceases nest building for a few days only, viz. from the time that the young are old enough to fend for themselves and undo the female's handiwork (± 19 days) until the birth of the new litter (± 24 days after the birth of the previous litter) (Johnson & Oliff, 1954). Before parturition the cage is cleaned out and all refuse, including old nesting material, deposited outside. The floor is cleaned by an action similar to that used in digging. Large objects are carried in the

Fig. 3. Smoothed daily activity curves of the laboratory bred animal (B). Continuous darkness. Table 4c. (1) 4th—5th June. (10) 13th—14th June.

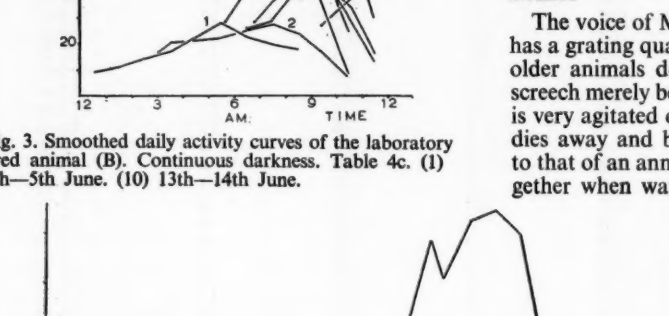


Fig. 4. Comparison of the activity curves of the laboratory bred animal (A) (unbroken line) in summer and the laboratory bred animal (B) (dotted line) in winter.

mouth. The forepaws are used to push refuse out of the cage. There is a notable tendency to push refuse upwards out of the roof of the cage despite the presence of holes in the floor. This is possibly a relic of life in a burrow.

Parental Care

Most Mastomys females are more aggressive with first litters and the survival rate increases with the number of the litter, since during excitement the young are frequently killed and eaten by the female; if sand is present the dead may be buried.

For the first few days the female remains with the young most of the time and hurries back to them at the least noise from the litter. The male does not share the nest except when cold but remains at the entrance. Offspring are old enough to fend for themselves at about 19 days but are still tolerated by the parents and there is no fighting even after the next litter is born.

Sounds

The voice of Mastomys is a harsh screech and has a grating quality. Young animals squeak but older animals do not, even when in pain; the screech merely becomes louder. When Mastomys is very agitated or afraid, this screech frequently dies away and becomes a rasping noise similar to that of an annoyed cat. Several Mastomys together when warm and after having eaten, frequently twitter like chickens going to sleep. Feeding mothers often make the same sound when tending the young.

Mastomys chatters its teeth and this sound is generally associated with consternation. When picked up, Mastomys vibrates in the thoracic region and this vibration causes a low pitched purring noise. This noise is produced whenever Mastomys is apprehensive and is possibly an involuntary result of trembling from fear.

Handling

Because it was believed that Mastomys was untamable, in the early days of this colony the animals were handled with undue roughness. For weighing purposes the animal was grasped with a hand protected by a canvas mitten and the mitten then inverted so that the captive lay within the mitten cavity. At present, it is still the practice to handle these animals by grasping the base of the tail with rubber tipped ovum forceps. When seized by the tail some animals turn and climb up to bite the forceps. Many individuals can, however, be picked up by the scruff of the neck without being induced to bite.

For weighing and other purposes where the animal is required to remain immobile, it is placed on a shiny or transparent surface on which it can get no grip. A glass jar painted black

provides a retreat in which the animal remains, making no attempt to escape. This method, although providing a quieter animal, introduces the difficulty of subsequent extraction, and at present the flat shiny plate seems preferable.

Taming

Although Mastomys tends to be wild, suitable handling and selection will assist in the process of taming and such animals can be picked up with the ungloved hand, and do not bite unless provoked.

(*a*) Feeding and fondling has tamed two individuals to the extent that they could not be induced to bite. When placed ten feet or so away they would run to their attendant and climb up a trouser leg and crawl into a pocket. The pocket was never soiled and the animal would always come out to defaecate or urinate. These animals lived normally with other Mastomys and after a few days in a cage would again be as wild as any laboratory-bred animal. After some minutes handling they would again be tame.

(*b*) A fair amount of success was had by placing an individual in a basin of water and offering the hand as the only source of refuge. After several repetitions the animal is less ready to bite.

(*c*) Two animals were repeatedly changed from one cage to another, always by hand. These two animals also had their cage mates changed frequently: white mice and Mystromys being used. After this treatment it was found that if gently handled and not startled, these two animals did not bite readily and were quite gentle. They remained tame even after a long sojourn in the cage.

(*d*) It was found that the dilute animals were less nervous, and easier to tame and to handle than the wild type.

(*e*) Animals kept in the dark in quiet and not disturbed often, usually became much more restful. Although they still bite, they do not show escape behaviour.

(*f*) Two groups of Mastomys were handled frequently. One group was handled roughly and the other group gently. After a period of time both groups were equally tame. Both groups again became wild when not handled for a few days, but if a white mouse was kept in the same cage, neither group reverted to wildness.

Summary

1. Mastomys behaviour in the laboratory after twelve generations is consistent with its field behaviour; amicable towards its own species and other rodents and showing much escape reaction towards possible danger sources such as man.

2. Mature wild type laboratory-bred and recent captives were investigated under differing light conditions in an activity cage. A twenty-four hour-cycle is present with maximum activity at night. The activity cycle of laboratory-bred animals was modified and less stable than that of a recent captive. Differing light conditions affected the activity cycle of both animals. The results suggest that the recent captive has the stronger innate activity cycle.

3. The general activities of Mastomys are described and illustrated.

4. Certain methods used in taming are described.

Acknowledgments

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APPENDIX: DESCRIPTION OF ACTIVITY CAGE

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Apparatus

The apparatus used was originally designed to investigate the activity in rats (*Rattus norvegicus albinus*). The requirements were identical to those in the present investigation: the apparatus had to be capable of long and continuous operation without much attention from the experimenter and to provide permanent records. Four cages, made of a quarter-inch mesh and angle iron, were used to house the animals during the experiment. Each cage measured 6″ x 22″ x 8″ high. The four activity cages were housed in a cupboard, provided with an air vent for ventilation, while the temperature was thermostatically controlled at 70°F. to within a few degrees. When the doors of the cupboard were open it received light from a north-facing window and total darkness was obtained when the doors were closed. Artificial illumination was provided by a clear 100-watt lamp, three feet above the cages.

The chassis with the amplifier as well as the kymograph drum were situated outside this cupboard so that the animals being tested could be undisturbed for as long as required except for feeding routines.

A beam of light is passed across the activity cages, about one inch from the floor, and falls on a photoelectric cell. When this beam is interrupted, light ceases to fall on it so that no current can pass. Conquently the thyratron no longer conducts and the relay opens. When the relay opens, current is fed to the electro-magnetic marker which thus makes a mark on the smoked paper on the kymograph drum. The kymograph drum moved in a spiral so that a very long record could be made. This arrangement permits the time of occurrence as well as the number of the interruptions of the beam to be recorded. The kymograph drum used in this investigation has been calibrated and was found to be extremely accurate over long periods, so that a further time line was unnecessary.

Thanks are due to Mr. H. Rubin for the basic amplifier design.

THE ROLE OF DENSITY IN AGGRESSIVE BEHAVIOUR OF HOUSE MICE

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Since the manifestation of territorial behaviour may be related to density, experiments were designed to compare the behaviour of mice at two levels of population. A number of discussions of territorialism have been published for several mammalian species (Burt, 1943; Yerger, 1953; Tanaka, 1953; Hediger, 1950) and recently Crowcroft (1955) described what he called "territorial" behaviour in house mice. None of these descriptions show territorialism in the narrow avian sense of the defence of a breeding area by posturing, song, and fighting. The observations on mammals usually show that the individual remained in an area and that others rarely entered but that not all individuals have a territory. Thus the relation to density is by no means clear. For birds, territorial behaviour is clearly related to density. In tropical areas, the individuals of some species may be so far apart that they rarely have a chance to manifest territorial behaviour (Davis, 1941) except in song which often is weak and infrequent. Numerous reports for birds show that territorial size decreases as density increases. At the end of the scale of increasing densities occurs a shift from territorial to social rank behaviour, for example, in doves (Bennett, 1942). This shift occurs also in some fish (Fabricius & Gustafson, 1954).

Methods

To clarify the relation of territorial behaviour and social rank behaviour in mice, an experiment was devised to observe the same mice at two densities. In this paper density is used in the strict sense of animals per unit of limiting factor. Space was the limiting factor and therefore was varied to produce a change in density. The procedure was to arrange a colony of wild-strain house mice (*Mus musculus*) in a large cage in a room. On August 30th, 1955, 19 adult male and 24 adult female mice were put in a cage. The mice were toe-clipped for individual identification. The cage was $6' \times 4' \times 1{\cdot}5'$ and was constructed of hardware cloth with cardboard sheets on the wire floor. Two water cups, excessive food (dog chow) and nesting material were available. For nests 12 quart glass jars were placed on their sides evenly spaced in a grid on the floor of the cage and labelled from A to L inclusive.

On 33 occasions (usually twice daily) from 2nd September to 3rd October the number of mice per jar was counted by looking through the glass, but the individuals were not captured and identified. On 11th October the mice were all captured and weighed. Four females and 1 male had died. From several litters only 2 females and 1 male had survived to reach a size of 14 or more grammes.

On 11th October these mice (now 19 males and 22 females) were liberated on the floor of the room in which the cage had been kept. The room was $14' \times 16'$ and contained two drinking cups and the same 12 jars placed in a grid. The floor was covered with shavings and food in excess was scattered about. Thus in terms of area the density was changed from 43 mice in 24 sq. ft. to 41 mice in 224 sq. ft. or reduced to about one-tenth. To reduce the likelihood that water was the limiting factor another cup was added in late October. From 14th October to 2nd November the number of mice in each jar was counted a total of 23 times as before.

The reason for simply counting the mice in a jar was that these data could be obtained without handling the mice and thereby disturbing them. Obviously, the location of individuals could not thus be determined. To remedy this deficiency from 7th to 30th November on 4 occasions the mice were captured from the jars and the location of each individual recorded.

To explore further the effect of space, on 7th December a set of baffles was placed on the floor. Six-inch boards were set lengthwise vertically so that 9 squares were produced and 13 jars and 2 water cups were added. Six counts of the individual mice were made from 9th December to 7th February, when the colony was collected, weighed and destroyed.

This colony was purposefully organised to have both sexes in order to resemble normal conditions of behaviour. But the reproduction produced some problems. Actually pregnancies regularly occurred but survival of young was trivial until January, 1956, when the population had declined due to death of some adults which were now about 9 or more months old. The vari-

ability produced by reproduction may have increased the variability of behaviour. A few deaths occurred during the work and may have contributed to variability

The actual procedures followed are deficient in some respects because certain objectives were mutually incompatible. Thus frequent capture of mice to identify individuals would have disturbed the colony (a scheme of marks visible at a distance was not feasible in this case). For this reason some of the analysis below has to be a bit devious. The total number of mice in jars does not equal the total in the colony at any particular time because some mice might be wandering around when the count was made.

Results

The data will be analysed from the view point of the number of animals per jar under the various conditions. The number per jar is considered a reflection of the ability of an individual to repulse individuals from his area. Table I gives the mean number of mice per jar and the standard deviation for each jar. The table is arranged with an increasing number of mice per jar. The mean number of mice per jar was less (2·82) in the cage than in the room (3·32) indicating that when within the cage, a number of mice were not in the jars and thus were running around a large part of the time. The number of mice in each jar showed a very similar distribution for the two densities. One jar rarely had a mouse, three jars usually had one mouse, three jars usually had two mice. But in the room a large number of mice clustered in one jar (J) which accounts for most of the increase in average per jar.

Table I. Mean Number of Mice per Jar Within Cage and Within Room

Within cage			Within room		
Jar	M	SD	Jar	M	SD
B	0·25	0·12	F	0·39	0·48
E	0·82	1·10	E	1·01	0·62
I	0·90	0·90	K	1·13	0·75
C	1·33	1·64	H	1·24	0·86
F	1·60	1·54	L	1·61	1·55
D	2·00	1·32	D	2·23	0·83
G	2·10	2·34	B	2·40	1·35
K	2·67	2·04	G	3·48	1·82
J	3·67	3·00	I	4·76	1·23
A	5·33	2·22	C	4·80	1·31
H	6·36	2·64	A	7·10	1·62
L	6·82	2·71	J	9·74	2·24

However, the standard deviations seemed much greater (Table I) when the mice were in the cage than when in the room. The variance for the mice in each jar were pooled and a value of F determined. The result was highly significant indicating that the number of mice per jar differed from count to count more in the cage than in the room. Thus the mice, when in the room, were more stable in their distribution than when in the cage.

In several cases after the mice were in the room, 1 mouse inhabited a particular jar for some time but then several more were found for the rest of the time. For example, jar K from 14th October to 28th October had one mouse on 13 occasions, O once and 2 once. But from 31st October to 4th November there were 6, 4, 3, 2, 2, 3, 4, 4 mice in the jar. Other jars had a series of single occupancies. Thus an average different from 1·0 can occur even though the jar was inhabited by one mouse for much of the time.

Because this type of analysis has the obvious disadvantage of failing to demonstrate that the same mouse was in the jar, individual examination of the mice was made at weekly intervals in November as explained above. Some males remained in the same area for several weeks. One mouse was caught in the same jar on all of 6 observations from 9th December to 7th February. However, he was not alone, for 2 other males were present. Males remained in the same area much more than did females. A comparison of location of capture in successive weeks shows that 64·3 per cent. of 49 captures of males were in the same place as the previous capture whereas only 27·2 per cent. of 22 captures of females were in the same place.

The sex composition of the mice in the jars needs consideration. During November there were 53 observations of males in jars and 55 of females. In 11 cases males were alone in a jar and in 2 cases females were alone. In one case 2 males were in a jar, in one case 2 females and in two cases a male and a female. It is apparent that the males tended to remain alone while the females tended to occur in groups. For example, a group of 8 contained only one male.

After the baffles and more jars were placed in the room there were 27 jars and 23 mice. On three occasions the mice in the jars were counted giving a total of 34 male and 37 female records. In 14 cases a male was alone in a jar and in 4 cases a female was alone. Once a male and female were together and three times two females were together. As before the large groups were predominately female. It is curious that, although there were fewer mice in the colony (it had decreased from about 35 to 23) after the baffles were placed, the maximum size of the groups was larger (9, 11, 11) than before (7, 7, 8, 7).

From the above discussion it seems likely that the insertion of baffles and more jars permitted more males to have a single jar for themselves. Also the females tended to be found singly more often.

Discussion

The results here reported suggest that males remain isolated in an area for some period of time and that when density is decreased, more individuals remain alone. Observations of mice during this experiment showed regular fighting and chasing. These results agree closely with Crowcoft (1955) who emphasised the observation of behaviour. He found that individual mice, usually males, defended an area against others.

A real problem is to decide how to interpret and what to call this behaviour. The word territory has been used to refer to the defence of an area and is generally recognised to have a definite meaning for birds and for some other vertebrates. The behaviour of mice is certainly defence of an area but it has complications. As density increases the number of areas defended decreases till eventually none is defended, at least successfully. Furthermore, at all times many individuals do not defend any area but group together.

Some observations from other work seems pertinent. When 6 male mice are put into a round can (about 2′ diameter) they will promptly fight and develop a social hierarchy. The top mouse however, will often stay on one side of the floor and the other 5 will huddle on the other side. Occasionally the top-ranking mouse would go over to the group, scatter them, and settle down somewhere else. Thus if there existed a "territory" it moved with the mouse, perhaps as described for geese by Jenkins (1944). This seems to be the "individual distance" concept explored by Marler (1956) for Chaffinches.

The relation of territory to social rank has puzzled zoologists for many years and this paper can not settle the question. However, an hypothesis for testing may be advanced: territorialism and social rank are two poles of a continuum of behaviour that is dependent upon density. At all densities the individuals arrange themselves in a rank but at low densities the groups tend to be smaller so that at the lowest density each "group" consists of one animal who thus has a territory and who is naturally dominant. The animals in a group tend to disperse according to the extent of fighting and each species has a particular level of dispersion. Thus mice do not disperse readily but can become submissive and form groups. In contrast, many birds such as Kingbirds, disperse promptly and never form groups. Some birds, such as the Anis, live in groups and have only a weak dispersal force. Some primates (Howling Monkeys) are very similar.

There is not enough evidence yet to warrant a detailed review of the many observations that might indicate the validity of this hypothesis. Many observations have been discussed by Armstrong (1942). However, it should be pointed out that an observation reported above seems contradictory. Even after the density was greatly decreased by baffles and jars, large groups of mice remained. Apparently the density was still not low enough for each mouse to have a jar.

In concluding this discussion it seems desirable to indicate what future experiments might be useful to explore this hypothesis and how to overcome some of the deficiencies in these experiments. The major problem was the difficulty of identifying individuals in large groups without disturbing them. This might be solved by combinations of dyes. Another problem is the disturbance of young. This could be solved by hysterectomy or gametocides which should leave the female behaviour normal. The possibility of seasonal change (admittedly remote) should be ruled out by starting experiments at various times of a year.

Summary

To examine the relation of aggressive behaviour to density, House Mice were placed in a cage and then in a room, each containing excess food and water. The density thus was reduced to one-tenth. Twelve jars were present in the cage and room and the mice in each jar were counted at intervals. The variability in the number of mice per jar was significantly greater in the cage

than in the room. Subsequently more jars were added to the room and more mice were found singly in a jar although some mice were still in groups. Some observations showed that individual mice remained in one jar for several weeks.

The hypothesis is suggested that territorialism and social rank are two poles of a behaviour continuum related to density, but the density is limited by a specific tolerance. At low densities individuals are territorial but at high densities they may associate into groups which have a social rank. But in some species the "individual distance" tolerance limit is so low that individuals can never associate together.

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ALTERNATIVE MOTOR PATTERNS IN CHAFFINCH SONG

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Introduction

Male Chaffinches (*Fringilla coelebs*) often have more than one song type in their repertoire (Thorpe, 1954, 1956; Marler, 1956). These occur apparently as alternatives, following each other in the same outburst of singing, and thus presumably sharing causal factors. However, if they were true alternatives, the distribution of each type through a song outburst would be random, and this is not the case. The analysis given here indicates the complexity of the factors, internal and external, controlling the type of song given in any particular instance.

The Chaffinch has a relatively simple song consisting of a trill, often divisible into two phrases, and an end-phrase (Fig. 1a and b). It shows considerable individual and regional variation (Thorpe, 1954; 1956; Promptoff, 1930; Marler, 1952). Thorpe (loc. cit., 1958; see also Poulsen, 1951) has shown that first year males, kept in auditory isolation from adults from a few days after hatching, develop a rather simple song (the "isolate" song) which usually consists of a series of notes of about the normal length and descending in pitch, but with at most a very simple end-phrase. All further details are acquired by individual learning, but this is sufficiently selective to ensure that the bird does not normally acquire notes from other species.

Although Chaffinch song can be induced by injections of testosterone propionate (Collard & Grevendal, 1946; Poulsen, 1951; Hinde, in prep.) the short-term waxing and waning of song depends on internal factors which are not easily subject to experimental control. However, the frequency with which songs are given varies with time, and these fluctuations in rate can be used to establish relationships between rate (i.e. songs per minute) and other characteristics of the singing. Thus the mere recording of the temporal characteristics of the singing can give some indications about the factors governing the alternation of song types, though the information obtained in this way is of course far from complete.

With regard to the external factors controlling song, singing is normally confined to the territory, and also to certain song posts within that territory. Apart from these, the most important external factor is the song of rival males (Marler, 1956). Accordingly the effect of playing back recorded Chaffinch song on the occurrence of the various song types was also studied.

The relationships revealed by this study are likely to have a qualitative generality, but their precise quantitative characteristics are relevant only to the particular individuals and circumstances concerned. Accordingly no attempt has been made to state the general conclusions in other than qualitative terms.

Material

Four of the five Chaffinches used in this study had acquired their song repertoire as a result of training experiments designed to investigate song learning (Thorpe, 1954, 1956, 1958). In some of these a "song tutor"—a device for playing a particular song at frequent short intervals—had been employed. The birds used were as follows:

Bird A. Hand-reared from the age of *c.*8 days in 1954. Trained with a reversed Chaffinch song (i.e. a normal Chaffinch song played backwards) in March 1955, it developed both an isolate song (Song Type A/1) and a reversed song (Type A/2).

Bird B. Trapped as a juvenile in July 1951, and used as a control in a number of song-learning experiments. It developed two fairly normal songs, one having a rapidly repeated series of notes in the second phrase forming a trill, and a rather emphatic end-phrase (Song Type B/1, see Fig. 1a), while the other had a steady series of notes in the first two phrases (Type B/2, see Fig. 1b).

Bird C. Hand-reared from the age of *c.*8 days in 1955. Exposed to several courses of Tree Pipit (*Anthus trivialis*) song from the song tutor between January and March 1956. It developed an isolate song (Song Type C/1) and an abnormal song showing some of the pitch trends of the Tree Pipit song, but none of its note structure (Type C/2).

Bird D. Hand-reared from the age of *c.*8 days in 1954 and exposed to reversed Chaffinch song from the song tutor in March 1955. It developed an isolate song (Type D/1, in Fig. 1c) and a reversed song (Type D/3). When exposed to the singing of wild Chaffinches in the course of these experiments it developed an elaboration of its

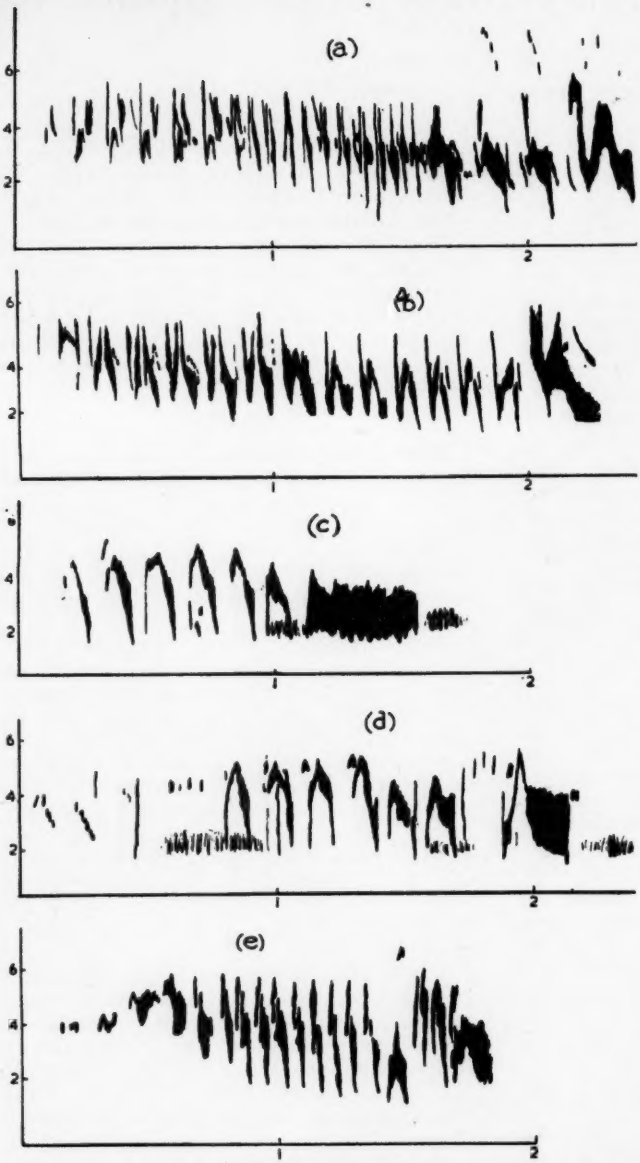

Fig. 1. Sound spectrograms of Chaffinch song. Ordinate—frequency in Kcs. Abscissa—time in secs. (*a*) and (*b*) Bird B. (*c*)—(*e*) Bird D.

isolate song which differed from the latter in having an end-phrase (Type D/2, see Fig. 1d). Later in the spring it developed yet another new song (Type D/4, Fig. 1e).

Bird E. Hand-reared in 1955 and exposed to normal Chaffinch song in November, 1955, and reversed song in the spring of 1956. It developed a song in which the first two phrases resembled normal Chaffinch song, but there was no end-phrase.

The differences between the songs in the repertoire of any one of the individuals A-D was thus greater than that between the songs of most individual wild Chaffinches, which are all recognisably "Chaffinch songs." (The reference numbers assigned to the various song types given above and in Fig. 1 are of course arbitrary, and no relation is implied between (e.g.) the Type 1 songs of different individuals).

These birds were confined in cages approximately 100 x 100 x 50 cm. in an open field: under such conditions they soon came into full song.

Normal Singing

"Normal singing" signifies singing when no recorded songs were being played back—other wild or caged Chaffinches may have been singing within earshot. It was studied simply by recording the time (nearest second) and type of each song given. Analysis of samples of normal singing from birds A-D permit the following generalisations:

(i) *The song types are not given with equal frequency*, some being more common than others. (Table I). In every case the observed frequencies differ from those which would occur if the song types were equally common with $P<0{\cdot}01$.

(ii) *The proportions of each song type may change with the rate of singing*. Furthermore, *the relation between the proportion of a particular song type and the rate of singing may change through the season*. The data for Bird A were collected over too narrow a range of rates of singing to show this effect. The data for Bird B were collected over a wide range of dates but with reasonably

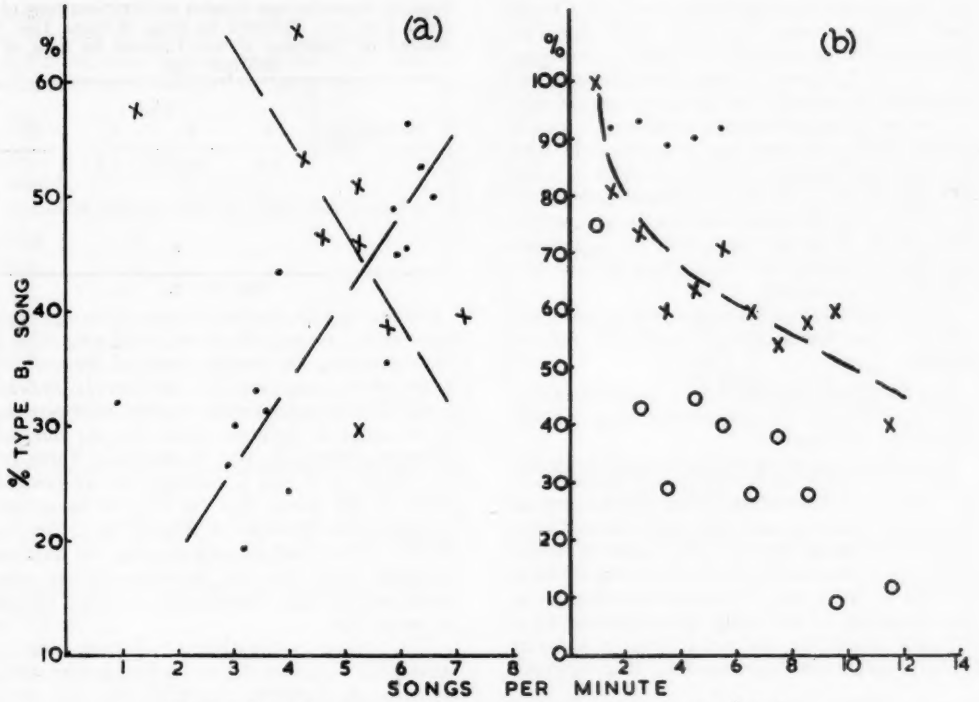

Fig. 2. Relation between relative frequency of song types and rate of singing.
(*a*) Bird B. Ordinate—percentage of type B/1 song. X period May 4th to June 12th. • period June 6th to 26th. (*b*) Bird D. Ordinate—percentage of D/1+D/2 songs to total number of all songs (X); percentage of D/1 to total D/1 + D/2, April 27th—May 3rd (0); percentage of D/1 to total D/1 + D/2, June 2nd—12th (•). Each point indicates mean for one watch (Bird B) or rate (D).

Table I. Percentage Frequency of the Various Song Types in the Analysed Samples

Song Type	Bird A	B	C	D
1	33·5	43·5	40·8	33·4
2	66·5	52·6	59·2	27·7
3	—	—	—	0·1
4	—	—	—	38·8
Size of sample (number of songs)	752	2180	1827	776

short watches on each day. The relation between the percentage of type B/1 songs on each day and the rate of singing changed during the course of the observation period as shown in Fig. 2a (Corrln. coeff. —0·62 (N=9) for the period May 4th to June 2nd, + 0·76 (N=15) for June 6th to 26th).

The data for Bird C were all collected within 4 days, but the watches were long and the rate of singing varied within each watch. Accordingly each watch was divided into 4-minute runs. The percentage of C/1 songs in each run decreased with increase in the total songs in that run. (Corrln. coeff. —0·34, N=85).

The data for Bird D were collected in two periods—April 27th to May 3rd and June 2-12th. The relation between the number of song types D/1 and D/2* in each run to the total number of songs in that run showed no change between the

*As shown in Fig. 1c and d, song type D/2 was closely similar to type D/1 in form. They were therefore treated together. In fact type D/1 can be regarded as an incomplete form of type D/2, its frequency becoming less relative to that of type D/2 as the rate of singing increased (Fig. 2b). Further evidence in favour of this view lies in the way in which they were intermingled in the song sequences (see below), the song-song intervals between types D/1 and D/2 and between types D/2 and D/1 being no longer than between types D/1 and D/1 or types D/2 and D/2.

two periods, the correlation ($r = -0{\cdot}29$, $N=45$ runs) being just significant at $P<0{\cdot}05$. The relations between the proportion of type D/1 to types D/1 and D/2, however, were quite different between the two periods. For the earlier one the negative correlation between the number of songs in each 4-minute run and the proportion of type D/1 was significant at $P<0{\cdot}05$ ($r=0{\cdot}65$, $N=20$). The data for the later period differed significantly ($P<0{\cdot}01$) from the data from the former: within this group, however, there was no significant correlation between the proportion of type D/1 and the rate of singing.

Thus with all these birds the proportion of the various song types changed with the rate of singing.

(iii) *Each song is more likely to be followed by a similar song than by a dissimilar song.* This is shown by the ratio

$$\frac{\text{No. of times song of one type followed by song of same type}}{\text{No. of times this song type followed by song of different type}}$$

in Table II. χ^2 tests showed that the number of times that a song of one type was followed by a song of the same type exceeded that to be expected on a chance distribution of song types at $P<0{\cdot}01$ in every case. The songs are thus given in a sequence of one song type followed by a sequence of another, and not at random. (Marler (1956) gives similar data from field observations).

Table II. Ratio Between Number of Occasions Song of a Given Type was Followed by Song of Same Type to Number of Occasions it was Followed by Song of a Different Type

Song type	Bird A	Bird B	Bird C	Bird D
1	3·8	9·0	5·3	10·4*
2	9·7	13·2	8·3	
4	—	—	—	6·3

*See above.

(iv) *The average interval between two songs of the same type is roughly the same for all song types in the repertoire. The average interval between two songs of the same type* (*i.e. the intervals between songs in one sequence*) *is shorter than that between songs of different types* (*i.e. the intervals between sequences*). This is shown in Table III. For Birds A, B and C the data for all possible intervals are given, that for Bird B being split according to the rate of singing (p. 215). For Bird D, which had 4 types of song, the data are grouped into intervals between similar song types and intervals in which there was a change of song type.

The frequency distribution of song-song intervals for Bird A is shown in Fig. 3. The distri-

Table III. Mean and Median Intervals Between Songs

Bird	Interval between song types	N	Mean	Median
A	1—1	203	15·5	10·2
	2—2	439	13·7	9·5
	1—2	53	24·2	16·8
	2—1	45	34·4	19·5
B (songs per min. between 2.5 and 4.0)	1—1	86	15·4	13·4
	2—2	236	15·4	13·5
	1—2	36	24·4	22·0
	2—1	34	32·1	28·7
B (songs per min. between 4.1 and 6.6)	1—1	352	9·5	8·9
	2—2	396	10·0	9·3
	1—2	37	13·2	11·5
	2—1	41	14·4	11·4
C	1—1	627	12·2	8·5
	2—2	966	14·2	8·5
	1—2	117	22·9	15·3
	2—1	117	20·4	15·3
D	Intervals between similar songs	660	12·3	—
	Intervals between dissimilar songs	83	17·5	

butions for the other individuals were similar, and for each the variability of intervals between songs of different type was greater than that of intervals between songs of the same type.

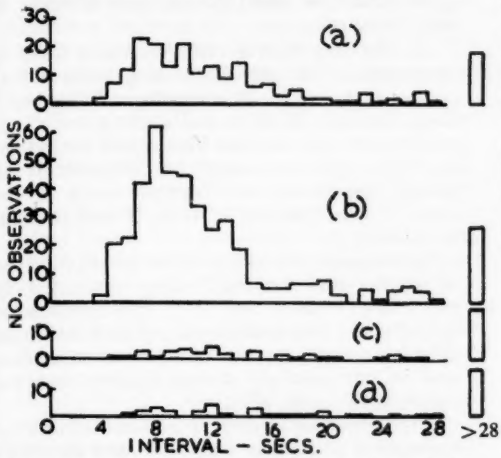

Fig. 3. Frequency distribution of song-song intervals for Bird A. (*a*) A/1—A/1. (*b*) A/2—A/2. (*c*) A/1—A/2. (*d*) A/2—A/1.

(v) As suggested by the data for Bird B in Table III, *the difference between the average interval between songs of the same type and the average interval between songs of different types decreases at high rates of singing*. This is shown directly by Bird B in Fig. 4. The data for Birds A, C and D were similar. In each case the ratio

$$\frac{\text{average interval between dissimilar songs}}{\text{average interval between similar songs}}$$

approached 1 at higher rates of singing, the decrease in the ratio being significant at $P<0{\cdot}05$ or better.

(vi) *The average number of songs per sequence increases with the rate of singing*. This is shown for the song type 2 of Chaffinch B, the type 1 of C and the type 4 of D in Fig. 5. The data for the other songs of each bird are very similar, and the increase in each case is significant at $P<0{\cdot}01$ or better.

This increase in the number of songs per sequence could be due to an increase in the duration of the sequence, a decrease in the song-song intervals, or both. The latter certainly occurs (see Fig. 4). The duration of the sequence is variable: with Chaffinch B it increased with the rate of singing, but with Chaffinches C and D there was no clear change in the mean duration

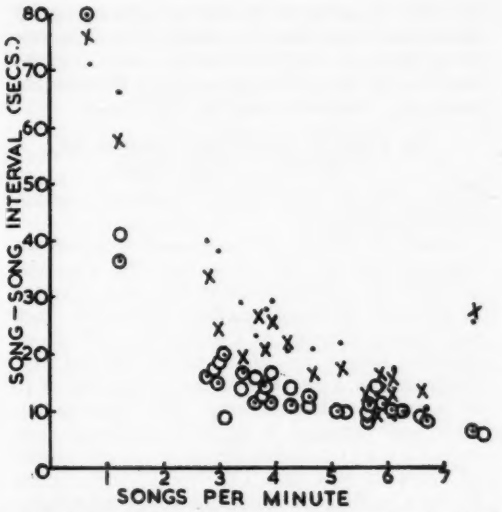

Fig. 4. Relation between song-song interval and rate of singing. Bird. B. (o) B/1—B/1. ⊙ B/2—B/2. X B/1—B/2. • B/2—B/1.

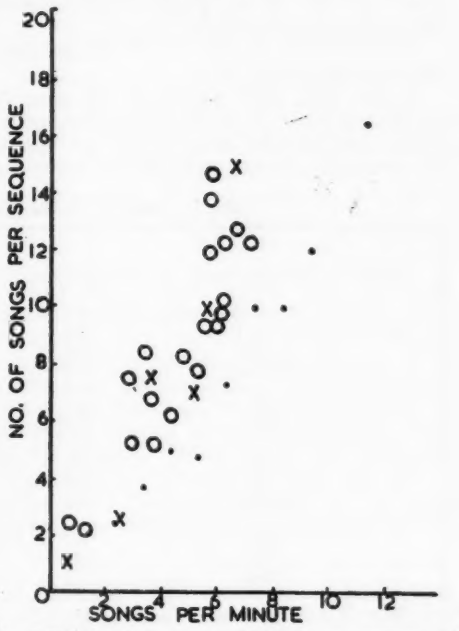

Fig. 5. Relation between rate of songs per sequence and rate of singing.

0 B/2. X C/1 • D/4.

of song sequences with the rate of singing. In these cases, therefore, the change over from one song type to another depends more on the duration of the preceding sequence than on the number of times the song has been sung.

The Effect of Played-back Song on the Proportion of Song Types

The response to records of Chaffinch song was studied as follows:

Each song which was to be used as a stimulus was recorded on disc. A second disc was then prepared on which the same song was recorded at intervals of approximately 15 seconds. Each experiment consisted of a sequence of 15 of one stimulus song from such a record, played over loudspeakers, a one minute gap, a sequence of 15 of a second stimulus song type, and so on. This was repeated a number of times, each stimulus song type being played an equal number of times on each day. The "reply" songs given by the Chaffinch to which the songs were being played was noted. (These are referred to here as "reply" songs though, in fact, they are not necessarily replies to particular stimulus songs: indeed the bird was nearly always singing before the experiment started.)

The results are shown in Table IV and can be summarised as follows:

(i) For each bird *playing of the song type which was given by the bird most frequently in normal singing* (see Table I) *was more effective in stimulating singing than playing other songs from the bird's repertoire.* The most effective songs were A/2 for Bird A, B/2 for Bird B, C/2 for Bird C. With Bird D, types D/1 and D/2 together (see footnote, p.) were more frequent than D/4, and D/2 was more effective in stimulating song.

(ii) *The song from a bird's repertoire which is most effective in stimulating song when played back is not related to its resemblance to "normal" song.* Thus for Birds A and C the more effective Type 2 songs were less like normal songs than the Type 1 (isolate) songs. (No judgment of the relative similarities to "normal" song of the songs in the repertoire of Birds B and D could be made.)

Furthermore, with three birds the effectiveness of playing back "normal" song was tested. In two cases (Birds A and E) it was significantly less effective in stimulating song than the more effective song from the bird's own repertoire, and in one case (C) it was slightly, but not significantly, more effective.

(iii) *When the singing is in some measure a response to a stimulus song type from the bird's own repertoire, the proportion of that song type tends to increase.* This is shown in the last two columns of Table IV, where the number of Type 1 (in the case of D, Type 1 and Type 2) replies to each stimulus song type is shown. With Birds A, B and C the proportion of Type 1 replies was significantly greater when Type 1 was used as a stimulus song than when Type 2 was used. With Bird D the proportion of Type

Table IV. Effect of Playing Stimulus Songs on the Bird's Own Singing

Bird	Stimulus song	No. of replies	Difference from equality significant at P<	No. of type 1 replies	Difference signficant at P<
A	A/1	158	0·001	76 (48%)	0·001
	A/2	242		56 (23%)	0·001
	Normal	162		59 (36%)	
B	B/1	403	(0·7)	267 (67%)	0·05
	B/2	435		217 (50%)	
C	C/1	481	0·001	193 (40%)	0·001
	C/2	557		162 (29%)	0·001
	Normal	581		245 (42%)	
D	D/1	511	0·001	314* (61%)	0·05
	D/2	571		336* (59%)	
	D/4	511		289* (56%)	
E	Own song	573	0·001		
	Normal	427			

*Totals refer to Type D/1 plus Type D/2

D/1 plus Type D/2 replies was significantly greater with Type D/1 as stimulus song than with Type D/4. The difference between D/2 and D/4 was in the same direction, but not significant.

With Birds A and C there was no significant difference between the proportion of Type 1 replies when normal song was used as the stimulus song and the proportion which occurred in normal singing (Table I).

Although the effect of playing a given stimulus song on the proportion of that song type as demonstrated in these experiments was not large, this may be due to the particular length of the sequences of stimulus songs. Further, in nature the use of a particular song type towards a rival would become accentuated by conditioning to stimuli other than the rival's song (e.g. landmarks).

Marler (1956) has stressed that when two wild Chaffinches sing against each other, they do not counter song with song, but each sings in its own rhythm, so that they soon get out of step. A similar conclusion was reached from these experiments—the reply songs were distributed almost at random over the 15-second interval between stimulus songs, with at most a slight concentration in the period 3-8 seconds after the stimulus song. The tendency to reply with a song similar to that being played is thus to be regarded not as a process of imitating the pattern just perceived, but as a facilitation of one of the "alternative" motor patterns in preference to the other(s).

Discussion

The data summarised in the preceding sections have implications concerning three problems:

(i) The Complexity of the Factors Underlying the Alternation Between Song Types

(*a*) The frequency of singing fluctuates during the course of each song outburst. Such fluctuations have not been studied here, and must be ascribed to as yet unanalysed fluctuations in the variables underlying singing or in other interfering activities.

(*b*) Since an interval of less than 3 seconds between songs is extremely rare, it may be suggested that each song is accompanied by an inhibitory effect on singing which is dissipated with time. That this inhibitory effect is a consequence of performance seems probable from the fact that the song-song intervals after the occasional incomplete songs tend to be shorter than those after normal songs; but it could be peripheral, or central, or both.

(*c*) If this inhibitory effect acted on both songs equally, the mechanism of change-over between song types remains unexplained. If it merely affected the song type just uttered more than the others, alternation would occur more often than on a random distribution of song types, instead of less. It is therefore necessary to postulate the existence, during the course of each song sequence, of a persisting tendency to repeat the song last uttered: this we may describe as a facilitative effect.

This facilitative effect could be merely a consequence of slight differences between the motivational factors for each song type. On this view the alternation between song types would depend on fluctuations in these factors, resulting in a dominance of first one type, then the other. This would be in harmony with, for instance, the fact that in some cases the temporal duration of the sequences is independent of the rate of singing, and thus of the number of times the song has been uttered. Although no observations have been made on differences between the motivation of song types in the Chaffinch, Great Tit (*Parus major*) males sometimes use a different song when waiting outside the box for the female from that used in territorial disputes (personal observation).

However, since the birds studied here were confined in small cages, there were no obvious changes in the external world likely to produce a change in motivation other than the singing itself. An alternative possibility is that the facilitative effect is a consequence of performance. The alternation between sequences would then be due to a difference between the time constants of the decay of the facilitative and inhibitory effects. There are too many unknowns for it to be profitable to suggest a specific model along these lines, but most of the features of the song sequences discussed in the first part of this paper could be accounted for in such a way. The significant aspect of performance could be the act of uttering, a proprioceptive feed-back, or the auditory perception of the consequent sound pattern: the importance of the latter is suggested by the facilitative effect of the playing back of one song type on the production of that type.

(ii) Song Learning

The songs which Chaffinches A-D sang most often were also most effective in eliciting song when played back. Further, the songs which Chaffinches A and E had learnt to sing, although

abnormal, were more effective in eliciting song when played back than was normal song. Thus the process of learning a song type determines not only what song will be sung, but also what will be effective in inducing singing. While the learning of the motor pattern, and the acquisition of the mechanism whereby a stimulus song is responded to, could be independent processes, this suggests that they depend on the same initial stage—namely the development of a selective responsiveness to the stimulus song. This is in harmony with what happens in the development of full song, which Thorpe (1954) describes as "so to speak 'crystallising out' of the amorphous subsong," the transformation of subsong into song consisting largely "in the gradual dropping out of the extreme frequencies." What "crystallises out" is determined by what the bird has heard in the past, which must be retained in some way as a pattern towards which the song gradually develops. Indeed, some characteristics of the song are learnt in the bird's youth, before it is itself able to sing. Thus, as Thorpe points out, the learning is not in the first place the acquisition merely of a motor pattern, but of a receptory mechanism responsive to the song which is being acquired.

(iii) Functional Aspects

In nature, song attracts females and repels males: it plays an important role in the defence of the territory (Marler, 1956). Since song is more likely to evoke a response from another Chaffinch if it resembles that Chaffinch's own song (p. 216), there will be a selective advantage in developing a song type like that of one's neighbours. Since each territory-owning male is likely to have several neighbours, there will be an advantage in having several songs and in replying to a song of one type with a similar one. Further, it will be disadvantageous to develop a song markedly different from the normal. All this, however, assumes an initial variability between the songs of individuals: given variability, there is a selective advantage to individual males in developing songs like those of their neighbours. The significance of the initial variability is another question, but is presumably related to the role of song in permitting individual recognition at a distance: this is especially likely to be important in pair formation and the maintenance of the pair bond.

Summary

1. When a Chaffinch has more than one song type in its repertoire, each song outburst consists of a sequence of one song type followed by a sequence of another, and so on. Data concerning various aspects of the succession of song sequences in an outburst are presented. It is suggested that the uttering of each song is associated with both inhibitory and facilitative effects on the repetition of that type, and that differences in the decay constants of the effects govern the alternation of song types.

2. When songs are played back to a Chaffinch, those song types which it utters most frequently itself are most effective in evoking singing, irrespective of whether they resemble normal song. Further, the frequency of the song type played tends to increase in the bird's own singing. This supports the view that song-learning consists primarily in the acquisition of a selective responsiveness to a particular song type (or range of types).

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THE ABILITY OF WORKER HONEYBEES (*Apis mellifera*) TO LEARN A CHANGE IN THE LOCATION OF THEIR HIVES

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Introduction

Under natural conditions honeybees only change their home after swarming, but in beekeeping practice it is sometimes necessary to move colonies from one site to another. Beekeepers commonly suppose that when a colony is moved more than a few feet to a site that is within flight range of the old, many of the bees that have previously flown return to the old site of their hives and are lost (see Free, 1958). The present work is confined to investigating the ability of worker honeybees to learn the new positions of their hives in such circumstances.

Method

Before a colony was moved to a new site a number of its foragers were given paint marks to make them recognisable. To ensure that the bees concerned were experienced flyers, and not merely bees undertaking so-called 'play' or orientation flights, only those which returned to their hive entrance with pollen were collected. They were taken into the laboratory, anaesthetised, marked and then liberated a few yards from their hive. As soon as sufficient bees had been marked, the entrance to their hive was closed after flying had ceased for the day, and the hive moved to a new site. The next morning the hive entrance was opened and an observer recorded the time of departure and arrival of the marked bees which flew.

An observer is more prone to miss bees leaving a hive than entering it, because they sometimes leave too quickly to be identified. Consequently, when determining the number of bees that returned to their parent colony in any experiment only the records of those seen to leave were taken into account. After each experiment the colony was examined and the marked bees present recorded, so that most of the bees which had returned home but not been observed to do so were accounted for. Even so, some were probably missed, so the percentage of bees which returned to their hive in its new site in the following experiments may be higher than the figures indicate.

Results

Removal a Short Distance When Other Colonies are Close to the Original Site

In both the following experiments a group of five colonies was arranged so that their hives were in a straight row six feet apart from one another. All the hives were the same size, shape and colour and faced in the same direction. They were situated in a small meadow almost entirely surrounded by bushes and trees.

Experiment A

Pollen-gatherers from the colony (No. 3) in the centre of the row were marked. The entrance of this hive was closed at dusk on 25th April, 1956, and it was removed 15 yards to the rear of its original position. The next day sixty-seven marked bees flew from it but only two (3 per cent.) returned. The following morning (27th April) the four colonies left in the row were examined and fifty marked bees from Colony 3 were found in them, mostly in the two hives on either side of the position from which Colony 3 had been removed:

	Colony 1	*Colony* 2	*Colony* 4	*Colony* 5
Number of marked bees:	0	17	31	2

After the colonies had been examined on 27th April, Colony 3 was returned to its original position in the centre of the row. On 30th April all the colonies were again examined and forty-eight of the sixty-five bees which had flown on 27th April and not returned home were found again; eight of these bees were still present in Colonies 2 and 4 but the remaining forty bees (83 per cent.) had returned to Colony 3.

On 30th April Colony 3 was again moved after flying had ceased for the day to the site 15 yards to the rear of its position in the row. Sixty-eight marked bees flew from it the next day but only one returned; 47 of the remainder were found later in the day in the other colonies (nine in Colony 2 and thirty-eight in Colony 4).

Experiment B

This experiment was similar to the above, and performed in the same location, but with differ-

ent colonies. The centre colony (C) was moved backwards 15 yards and opened on the morning of 30th May, 1956. In contrast to experiment A an empty hive, with a closed entrance, was placed in the position formerly occupied by the hive housing Colony C. During 30th May, one hundred and ninety-one marked bees flew from Colony C but none returned and no marked bees were present in this colony at the end of the day. Many bees were seen at the empty hive during the day; some were exposing their scent glands and fanning at its entrance. (Similar behaviour was observed in subsequent experiments at both old and new sites, particularly at the latter). The next morning the four remaining colonies in the row were examined and one hundred and fifty-eight marked bees found in them:

	Colony A	*Colony B*	*Colony* D	*Colony* E
Number of marked bees:	0	47	111	0

In both this and the previous experiment the colony situated to the right of the centre position received the greater number of marked bees. In both experiments the main line of bee flight was towards the left of the row of colonies (i.e. in the direction E→A) and, on their return from foraging, many bees of Colony C flew in front of Colonies A and B, veered towards the position their colony had occupied and then entered the hive next along the row, which contained Colony D.

Colony C was moved back to its original site on 31st May, and on 1st June all the colonies were again examined for marked bees. Sixty-two of the one hundred and two marked bees found (61 per cent.) had returned to their original colony—Colony C. A week later, 28 of the 58 marked bees still present (48 per cent.) were found in Colony C, so the proportion of marked bees in Colony C had not increased. Thus, fewer bees returned to their original colony, when it was replaced in its old site, than in the previous experiment. This may have been because an empty hive had been placed in the centre position of the row when Colony C was removed and, consequently, the return of the original hive did not alter the configuration of the row as in Experiment A.

Removal to Various Distances Within Original Flight Range, no Other Colonies Being Close to the Original Site

Colonies were moved away from their original sites to distances of 5 yards, 15 yards, ¼ mile and one mile. In some experiments an empty hive,

Table I. Removal of Colonies to New Sites Within Probable Flight Range of Old

Experiment no.	Date	Distance moved	Whether empty hive at old site	No. marked bees flew	Percentage returned to new site	
1	30 Aug. 1956	5 yards	Yes	17	100	
2	19 Aug. 1957	„ „	Yes	40	90	Mean=94
3	14 Aug. 1957	„ „	No	46	98	
4	4 Sept. 1957	„ „	No	56	87	
5	18, 19, 20 April 1956	15 yards	Yes	176	69	
6	18 July 1956	„ „	No	126	78	Mean=81
7	14 June 1957	„ „	No	257	96	
8	11, 12 July 1956	¼ mile	Yes	174	76	
9	11 June 1957	„ „	No	145	85	Mean=82
10	29 Aug. 1957	„ „	No	55	85	
11	24, 25 July 1957	1 mile	Yes	191	75	Mean=83
12	20 June 1957	„ „	No	126	92	

identical with that housing the colony, replaced the latter at the original site. In such cases observers were continuously present both at the empty hive and at the hive housing the experimental colony. The majority of the experiments were carried out in apiaries, where, although other colonies were present, they were not within a radius of several yards of the old site. Optical landmarks were abundant at both old and new sites. The results of the experiments are summarised in Table I.

a mile or one mile, most of the bees returned directly to the new site, but when a colony was moved 5 yards or 15 yards, a high proportion of the bees visited the old one. However, in the latter experiments, relatively more of the bees which visited the old site subsequently returned to the new one, so as many bees eventually returned to their new homes as in experiments involving longer moves.

In Experiments 8 and 11 the colonies were observed on both the first and second day after

Table II. Behaviour of Bees Following the Removal of Their Colony to a New Site

Expt. no.	Date	Distance moved	No. marked bees flew	% returned to new site	% returned to new site without visiting old	% visited old site	% of the bees visiting old which subsequently returned to new	% did not return to new site and not seen at old
1	30 Aug. 1956	5 yards	17	100	23	76	100	0
2	19 Aug. 1957	5 yards	40	90	27	65	96	7·5
5	18, 19, 20 April 1956	15 yards	176	69	29	66	60	5
8	11, 12 July 1956	¼ mile	174	76	64	25	48	11
11	24, 25 July 1956	1 mile	191	75	69	19	33	13

Except when colonies were moved only 5 yards the presence of an empty hive at the old site appears to be correlated with a reduction in the percentage of bees returhing to the new. Probably, in such circumstances the bees were more attracted to remain in the vicinity of the old site.

However, the presence of an empty hive at the old site was advantageous in that the behaviour of the bees could be ascertained more fully. A summary of the data obtained is given in Table II

When a colony was moved either a quarter of

their positions had been changed, and in experiment 5 for three days. Marked foragers which flew from their hive at its new site for the first time on the second or third day of observation were no more successful at returning to the new site than those that flew on the first day (see Table III).

Most of the bees which visited the old sites of their hive arrived there after they had been foraging; many had pollen in their corbiculae. While at the hive in its original site bees spent

Table III. Return of Bees to a New Site

Experiment no.	Day of first flight from new site					
	Day 1		Day 2		Day 3	
	No. of bees flying	% return to new site	No. of bees flying	% return to new site	No. of bees flying	% return to new site
5	32	62	106	69	38	74
8	164	76	10	70	—	—
11	170	76	21	62	—	—

much of their time running along the alighting-board attempting to enter it, now and then leaving for short flights. The time a bee spent at the old site before she returned home varied greatly but, in general, the greater the distance separating old and new sites the longer a bee tended to remain at the old site. The mean times taken by bees to return to the new sites of their hives after arriving at the old ones were: Expts. 1 and 2 (5 yards moves): 13.1 minutes; Expt. 5 (15 yards move): 33·1 minutes; Expt. 8 (¼ mile move): 102·1 minutes; Expt. 11 (1 mile move): 112·8 minutes.

Approximately one-third of the bees visited the old site of their colony again, after they had returned from it to their new home; the proportion did not vary significantly in the different experiments. The behaviour of different individuals varied greatly; some returned to the old site before proceeding to the new at the end of nearly every foraging trip. Others returned directly to the new site for several consecutive trips, only to re-appear at the old one. This was particularly likely to occur on a bee's first trip of the day, even when the individual concerned seemed to have learned the new position of its colony thoroughly on the previous day. However, the number of bees visiting the old site diminished as an experiment proceeded. Thus, in Experiment 5 (observed for three consecutive days) 36 per cent. of the bees which returned home after visiting the old site on the first day, also visited the old on the second day, but only 9 per cent. of them visited it on the third.

All the above experiments took place under conditions favourable for bee flight. A further experiment, involving a move of 15 yards, was carried out on 6th June, 1957, in cold, windy weather. As the bees were reluctant to fly they were fed with sugar syrup inside their hives to induce them to do so. Ninety-three bees flew during the day but only thirty-nine (42 per cent.) returned home. Many bees searching at the old site became chilled and a cluster of them formed at the base of a tree-trunk nearby. The next morning many were dead and the remainder moribund.

Removal Beyond Original Flight Range and Then Back to Position Near the Old Site

After dark on 9th May, 1956, a colony was moved to a site five miles from its first one. During observations on 10th and 11th May, 143 marked bees were seen to leave their hive and 134 of them (94 per cent.) returned to it again. After flying had ceased on 14th May the colony was returned to a third site 15 yards away from the first one, where an empty hive had been placed. The bees were allowed to fly the next morning and observers were present at both the first and third sites. During the day 123 marked bees which had flown at the site five miles away left their hive; 112 (91 per cent.) returned to their colony at the third site, 83 (74 per cent.) without visiting the first one; 75 per cent. of the 28 bees which visited the first site eventually returned to the third one.

The percentage of bees which returned to the third site without visiting the first one was higher than when colonies were moved directly to a site within a short distance of the previous one (Table II).

Discussion and Conclusions

Bethe (1898), Wolf (1927), Butler (1949), and Ribbands & Speirs (1953) demonstrated that honeybees learn changes in the position of the entrances to their hives.

Simpson (1954) moved a colony 20 yards and put another colony at its old site. Most of the marked foragers in the moved colony returned to the old site of their hive and joined the strange colony there. The present data show that if there is no colony at the old site returning foragers attempt to enter any neighbouring colony in the *immediate* vicinity.

Most bees return to their hive when it has been moved to a new location within foraging distance of the old one, provided there is no other hive in the immediate vicinity of the old site.*

Many bees which eventually return to the new site of their colony first visit its old site, especially after short moves. There are two possible explanations of this: Opfinger (1931) showed that during departure-flights from a newly discovered food-place bees memorize its position relative to distant landmarks, its more immediate characteristics being learnt during subsequent approach-flights. Bees seem to behave in a similar manner when orientating themselves to their hives (Ribbands & Speirs, 1953). After a short move the relationship of a hive to its more distant optical landmarks may not change noticeably, so that many bees fail to orientate when leaving, and consequently return to the old position from whence they are attracted to the new position by scenting and fanning bees. A more likely explanation is that when old and new site are close

*The practical application of the results in relation to beekeeping are considered elsewhere. (Free, 1958).

together the bees appreciate the change in position of their hive when they leave, but on returning to the new site they are reminded of the position of the old one and fly there, as also seems to be the case with bumblebees (Free, 1955). Apart from memory of the new site, a honeybee's return to it would, no doubt, be facilitated by scent distributed around the hive entrance.

When a colony has been at a distant site for a few days, its bees may still remember and visit the original site of their hive when returned to its vicinity, although the proportion of bees that do so is less than if their colony had been moved directly to its final position. It is possible that removal to a distant site does not so much obliterate the bees' memories of the position of the old site, but that the previous move results in the bees becoming more adaptable to a change in the position of their home (see Ribbands & Speirs, 1953).

Summary

When the site of a colony of honeybees was changed, and other colonies were near the old site, nearly all of the bees which returned there from the new one attempted to join them. When there were no colonies near to the old site 69-100 per cent. of the bees returned to their colony in its new position, although many of them visited the old site first. Some bees also visited the old site on subsequent occasions; the behaviour of individual bees varied greatly.

The proportion of bees visiting the old site depended on the distance between old and new sites, and decreased with increase in the distance their colony had been moved. The greater the distance between old and new sites the longer bees spent at the old site before returning to the new one, and the less likely they were to return to the new one.

A colony was moved to a second site out of foraging range of its old one and then, five days later, returned to a third site 15 yards from the first one; fewer bees visited the first site than if the colony had been moved directly from first to third site.

Acknowledgments

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FURTHER STUDIES ON THE COURTSHIP BEHAVIOUR OF AFRICAN MIMETIC BUTTERFLIES

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The present paper is concerned with the behaviour of *Hypolimnas misippus* L., *Danaus chrysippus* L., *Papilio dardanus* Brown, and *Papilio demodocus* Esper. The information presented embodies certain experimental work carried out at the University College, Ghana, together with certain observations made in the Sudan. Although incomplete in themselves, they explain certain aspects of the behaviour of *Hypolimnus misippus* reported in previous papers (Stride, 1956, 1957). Preliminary experiments on the behaviour of the female of *H. misippus* provided interesting information, but this investigation had to be abandoned when the author left Ghana for the Sudan. The observations on the other species of butterflies are included as they may be of interest to other workers who may study the biological problems associated with the mimetic butterflies of Africa.

Hypolimnas misippus

Despite extensive observation of *H. misippus* during the course of the work described in the previous papers, the complete sequence of courtship and mating had not been observed in this butterfly under field conditions. Shortly before the author left Ghana a large flight cage was constructed with funds provided by the General Board of the Faculties of the University of the Gold Coast. This enabled the scope of experiments and observations possible on the behaviour of *H. misippus* to be extended. The cage measured 30′ x 20′ x 15′ high, the sides being made of green nylon mosquito proof gauze, and the roof of ¼″-mesh wire netting. In designing the cage it was realised that the butterflies would behave most "naturally" in a cage that permitted a maximum amount of light to enter from above and a minimum to enter from the sides. The use of mosquito-proofing in the sides was necessary to permit adequate ventilation to make the cage habitable under the tropical conditions of West Africa, but it did allow light to enter from the sides. Butterflies frequently appear not to recognise obstacles that allow light to pass through or that reflect a lot of light (they frequently try to fly through the whitened walls of houses reflecting bright sunlight), and in the flight cage they battered themselves by persistently fluttering against the upwind walls. This was prevented by fixing rush mats to the outside of the adjacent upwind walls. These mats broke the force of the wind and also rendered the walls visible to the insects. Rapidly growing climbing plants were placed against the other walls of the cage, and suitable flowering shrubs planted inside the cage. Under these conditions even large free-flying insects like the males of *P. dardanus* appeared to behave quite naturally and did not attempt to escape from the cage unless frightened.

Copulation of *Hypolimnus misippus* in the Flight Cage

Copulation of this species occurred readily in the flight cage as the following observations will show.

Under normal conditions the emergence of *H. misippus* from the pupa occurs during the first four hours of daylight. Although the females mated quite readily on the day of emergence, the males did not court readily until they had been out of the pupa for at least 48 hours. The following observations were therefore made with females that were at least 24 hours emerged, and males that were at least 48 hours emerged. Prior to their release in the flight cage they were kept in a dark room and fed artificially with sugar solution. The males are active insects, and even in a dark room it was not always possible to reduce activity sufficiently to prevent them damaging themselves in the small cages available.

Six female butterflies (24 hours emerged) were liberated in the cage one morning, and allowed to spend the remainder of the day undisturbed therein. During the following morning six males were introduced in turn. These males had been artificially fed during the earlier part of the morning in order to reduce their feeding activities to a minimum. After being liberated in the cage each male was allowed about five minutes

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to adjust himself to the new surroundings. A female was then gently disturbed so that she flew past the male. On each occasion the male arose in flight and commenced to court the female. Of the six males, two mated successfully on their first courtship, two on their second, and one on its third. The sixth male carried out three courtships, none of which was successful. The conditions provided by the cage were undoubtedly suitable for the courtship and mating of *H. misippus*.

Successful courtships were generally of short duration. The male would rise to follow the flying female and when he came near to her he would commence the quivering flight behaviour previously described (Stride, 1956). The flight of the female then became somewhat irregular, showing a tendency to pass into the quivering flight, so that she lost height and came to rest on the sides of the cage or on the herbage. At this stage there appeared to be a reasonably consistent difference between the behaviour of receptive and unreceptive females, the former holding her wings loosely open (thus exposing the rich golden-brown colour of the upper surface), the latter folding her wings tightly together above her back. The open wings of the receptive female appeared to stimulate the male to further activity so that he pushed his way forward underneath the female's wings, at the same time bending his abdomen sharply so that the genitalia were directed forward and able to meet those of the female. As soon as copulation occurred the male turned so that the insects were in the normal tail to tail position, and he then became cataleptic. The active partner in copulating pairs of *H. misippus* was always the female, thus supporting the suggestion advanced to explain the experimental catalepsis of the male noted in the earlier paper on *H. misippus* courtship.

With an unreceptive female, settled with her wings tightly closed, the activity of the male appeared to be immediately depressed. He would sit quietly beside the female, making no attempt to copulate with her. The two butterflies might sit quietly thus for as long as ten minutes, but, when the female again moved, the male almost invariably recommenced his courtship, and followed the female, quivering his wings. Occasionally, despite the closed wings of the female, the male would continue to try to copulate with the female, and this would eventually cause the female to fly away.

In the flight cage virgin females (and less frequently impregnated females) often escaped from the males in a characteristic manner by falling suddenly, with wings closed, from a height of 2-5 feet into the herbage below. Such females would remain quite motionless for several minutes with their wings closed. The males were very quick to follow this manoeuvre, and they frequently found the female again if she happened to fall into short grass or amongst thin open herbage. It appeared that this reaction of the female was a simple escape reaction, not necessarily associated with courtship, and it was sometimes seen in butterflies that had been successfully struck at with a butterfly net. In the latter circumstances the butterflies often enhanced their chances of escape by "falling" into the bottom of a bush. This type of escape behaviour appeared to be particularly strongly developed among certain forest-haunting species of Lepidoptera possessing apparently cryptic wing patterns.

The behaviour of the female butterflies in the flight cage explained the significance of the "ascending flight" response to the male which was described in the first paper on *Hypolimnas* courtship. This is a very conspicuous feature in the behaviour of free-living *Hypolimnas* females. When approached by a male they often commence the quivering flight but rise continuously to a height of some 30 or 40 feet, the male following below also with quivering flight. The female does not cease to rise until the male breaks off his pursuit and drops back to the ground. Observations in the flight cage indicated that virgin females rarely showed this ascending flight response. Fertilised females, however, when approached by a male, generally rose to the roof of the cage and might spend several minutes endeavouring to escape, all the while performing the quivering flight. The male would fly in similar fashion below them. There seemed little doubt that such females were endeavouring to carry out the ascending flight response, and that in the field this response is a means whereby the fertilised female may escape the persistent attentions of the males. It is noteworthy that although the ascending flight reaction appears to be a courtship-avoiding response of fertilised females, it nevertheless contains an important element of the courtship behaviour, i.e. the quivering flight.

The Role of Visual Stimuli in the Courtship Responses of the Female *Hypolimnas misippus*

Since there is little information available on

the active part played by the female in the courtship of butterflies, particular interest was attached to the effect of visual stimuli on the female. Only preliminary experiments on this subject were possible, but they indicated that visual stimuli are important in evoking the appropriate courtship responses from the female, and this itself is worthy of record.

The most convincing and conspicuous examples of butterfly mimetism are those in which the mimetic species have developed a wing pattern and pigmentation very different from that found in the more typical members of their genus. In this respect the African mimetic butterflies fall into two distinct groups; one group in which both male and female have acquired the new mimetic pattern, and another group in which only the female has evolved the mimetic pattern. Thus, considering two mimics of the polymorphic *Danaus chrysippus*, *Acraea encedon* L., has developed appropriate mimetic forms in both sexes, while *Hypolimnas misippus* has developed mimetic forms only in the female. This sexual dimorphism remains one of the more puzzling biological features of the mimetic butterflies. Certain of the explanatory hypothesis advanced (Carpenter & Ford, 1933) do not appear to show appreciation that the general principles of protection underlying mimetic colouration are similar to those underlying protective cryptic colouration. In both cases the insect is protected by resemblance to some inedible object in the same environment. Certain of the hypothesis put forward to explain the sexual dimorphism of mimetic butterflies would appear to apply equally well to cryptic butterflies; yet sexual dimorphism is not a noticeable feature of cryptic butterflies. Thus the presence or absence of sexual dimorphism in these insects seems to be related to the nature of the object that is used as a model, and to be associated with some biological difference that exists between (*a*) the leaves, stones, flowers, etc., that form the models for the cryptic butterflies, and (*b*) the distasteful insects that form the models for the mimetic butterflies. Among the more obvious biological differences is a difference in mobility, cryptic butterflies generally showing a resemblance to immobile objects and therefore showing a high degree of immobility themselves. A mimetic butterfly, by contrast, will in general only derive an advantage from its mimetic colouration when it is active, and thus it would seem that predatory pressure and selection on mimetic colouration is likely to be more rigorous than on cryptic colouration. Presumably a butterfly-eating predator sees an active mimetic butterfly as potential food and then has to "decide" whether the butterfly is likely to be edible or otherwise—the immobile cryptic butterfly is seen by the predator as something inedible and not warranting closer investigation. Even if mimetic butterflies do undergo more intensive predator selection than do cryptic butterflies, it is difficult to see how this could result in the development of a sexual dimorphism more readily in the one than in the other.

A second biological difference between the models of mimetic butterflies and the models of cryptic butterflies concerns their evolutionary change during the evolution of the butterflies. The models of cryptic butterflies are often inanimate and these will have shown no evolutionary change. When the cryptic similarity is acquired to an organic object, it is usually of a generalised nature, e.g. to withered brown leaves in general rather than to withered brown leaves of any particular species. Thus the organic models of cryptic colouration, like the inorganic, are unlikely to have undergone much change in their nature during the evolution of the butterflies concerned. It seems possible, therefore, that a cryptic butterfly might evolve its wing pattern slowly over an evolutionary long period of time.

In contrast to the slow rate of wing pattern evolution adequate to produce a cryptic wing pattern, the rate of evolution associated with the production of the female wing pattern in the sexually dimorphic mimetic species of butterflies may well have been more rapid. Thus *Papilio dardanus* shows a series of mimetic forms only on the mainland and associated islands of Africa. In Madagascar the males and females of this species are tolerably similar to each other and to the males of the mainland races. This suggests that the wing pattern of the species as a whole had been established in the general cream and black form, characteristic of all the modern males, before the isolation occurred which now separates the Madagascan from the mainland races. The mimetic patterns of the mainland females have presumably been evolved at a rather later stage in the evolution of the species. Considering *H. misippus* the male carries a pigmentation and pattern that is of the same basic type (black with white patches) as is found in most other members of the genus. This again suggests that the species shared a common ancestry with other members of the genus up to a comparatively recent time and that the development of the

mimetic female has taken place since *H. misippus* separated from other members of the genus. Thus, in order to acquire a mimetic pattern it is likely that some, at least, of the modern sexually dimorphic butterflies had to undergo a radical change in pigmentation. This change in pigmentation (*as opposed to change of pattern*) may well have occurred in the form of sudden well-marked mutations since comparatively small changes in the chemistry of physiological pigments may have quite profound effects on their colour. Such small physiological effects may result from comparatively small differences in the genetical make-up of the individuals concerned. If it is accepted that the pigmentary changes necessary to acquire a mimetic resemblance may well have arisen suddenly, then a subsequent sexual dimorphism might have arisen as a result of one sex showing a greater sexual selection against an abnormally coloured mate than did the other. To produce the situation now found in the African sexually dimorphic butterflies, it would be necessary for the females to show a greater sexual discrimination against "mimetic" males than *vice-versa*, thus allowing sexual selection to oppose change in the male wing pigmentation, while mimetic selection encouraged further change in the female wing pigmentation. The role of visual stimuli in determining the responses of the female *Hypolimnas* to the courting male is obviously relevant to this hypothesis, and an investigation into this aspect of the butterfly's courtship was commenced. The author left Gold Coast, however, when only a few preliminary experiments had been completed.

In the first experiment, nine males, which had emerged two days previously, were in turn liberated into the flight cage. The cage contained virgin females, and brief notes were made on each courtship that occurred. Before liberation the males were treated as follows:

Males A, B. The white spots on each wing were painted out with chlorazol black solution. Although this treatment removed the white spots it did not affect the blue irridescence, which continued to shine through brightly. "*Black males.*"

Males C, D, E. As much scaling as possible was removed from the wing without damage to the wing membrane. "*Colourless males.*"

Males F, G, H, I. Normal males, untreated in any way. "*Control males.*"

In each experiment six virgin females were present in the flight cage, mated females being replaced as necessary.

Male A (Black). The first female approached by this male continued to fly unhurriedly round the cage for 13 seconds before settling on a bush. After the male had fanned the settled female for a few seconds with his wings, copulation occurred.

Male B. The first female courted flew away and tried to escape by falling to the ground on three occasions, the third occasion being successful. The total pursuit time of the male was about forty seconds.

The second female approached and flew about in acquiescent flight (i.e. rather slow, but with a marked tendency towards the quivering flight) for about a minute, after which she settled. The male settled beside her and copulation was almost immediate.

Male C (*Colourless*). The first courtship lasted for about 35 seconds. The female made no attempt to escape but also showed no signs of settling, and the male ceased to court. The 2nd-5th courtships with other females were rather similar, and unsuccessful. The female involved in the sixth courtship appeared to be frightened and escaped by falling into a bush. The 7th and 9th courtships were also unsuccessful, although one of the females concerned did settle several times. Each time the male tried to copulate, however, the female flew away again. (Two further courtships carried out by this male on the following day to this experiment were likewise unsuccessful).

Male D. This male had six unsuccessful courtships of half to two minutes duration each.

Male E. This male had one unsuccessful courtship before being caught in a spider's web.

Male F (*Control*). The first courtship was successful after 54 seconds.

Male G. The first courtship was successful after 29 seconds.

Males H and I. The first courtships were successful in each case.

The above results may be summarised thus:

Type of male.	*Number of males.*	*Number of courtships.*	*Number successful.*
Control	4	4	4
Black	2	3	2
Colourless	3	18	0

Although the number of males used was small, there was little doubt that there was a marked difference in the reaction of the females to colourless males as opposed to black or control males. It also seemed that the white spots on the wings of the males played little part in the courtship of the butterfly; presumably the important visual stimuli arose from the black areas of the wings.

Other evidence of an unexpected nature was also noted which indicated that specific visual stimuli arising from the male wings were important in eliciting the courtship responses of the female. When virgin females were confined in the flight cage in the absence of males for several days, many of them showed a change of behaviour. They would then fly up behind other passing females and follow them, all the while performing the quivering flight. This behaviour was so similar to that of the male that one felt that the absence of any response by the pursued female must be due to the absence of certain visual stimuli. (Evidence has been presented (Stride, 1956) that as far as the male is concerned sexually significant scents in this species are found in both sexes).

Danaus chrysippus

The complete courtship and copulatory behaviour of *D. chrysippus* has not been previously described. This is perhaps not surprising since, although it is a very common and widespread species, it is, like many other Danaids, of a somewhat gregarious nature. Obviously such a gregarious tendency in a butterfly must be associated with a suppression of courtship tendencies, and observations on the behaviour of this species in the flight cage suggested that the males rapidly became habituated to the presence of the females. It is uncertain to what extent the natural aggregations of *Danaus chrysippus* are the result of the butterflies collecting in a particularly favourable environment, and to what extent they depend on an innate gregarious tendency of the species. Certainly during the greater part of the day the butterflies appear to be little affected by each others presence, and positive behavioural responses of one individual to another, though not infrequent, do not appear to represent the normal behaviour of the species. It should be noted, however, that when *D. chrysippus* is encountered in active groups during the day, the butterflies are usually feeding, and also that the two sexes fly preferentially at different times of the day. Thus collections made in the morning and afternoon from the same feeding ground generally showed an extremely significant difference in the sex ratio. When the butterflies are settling down to roost, and have ceased feeding, they frequently show a genuine gregarious tendency. Thus, on one occasion in Ghana nearly two dozen individuals were found roosting on a single spray of tall grass. When disturbed the butterflies flew around for a few minutes and in time all assembled together again on a neighbouring grass spray. Observations were also made on the roosting of this species in the neighbourhood of Khartoum in Sudan. Each evening the butterflies were seen to congregate by a long pile of brush wood on the banks of the Nile. One or two individuals would settle to roost but the majority continued to fly around the brushwood until they located a roosting butterfly, beside which they then settled to roost. In this way the roosting butterflies became associated in little groups of up to six individuals.

The courtship of danaid butterflies is likely to prove of considerable interest as specialised structures, associated with courtship, have been developed in the males of this group of butterflies. These structures are the abdominal brushes, and the sexual spots on the hindwings.

The sexual spots occur only on the hindwings of the males. They may be simply small areas of the wing in which the membrane has been thickened and the scale structure modified in order, it seems, to permit secretory activity (Eltringham, 1916). In *D. chrysippus* the wing membrane has been further modified to form a small pocket which contains and protects the secretory (?) structures. The anal brushes are eversible structures found in the male abdomen. When extruded they are each seen to consist of a haemolymph-filled stalk bearing a terminal spherical mass of comparatively long hairs. In *D. chrysippus* the hairs are dark coloured and all of the same type, but in some species more than one type of hair is found, Since certain danaid butterflies have been observed to rub the anal brushes over the sexual spots (e.g. Lamborn, 1922; Poulton, 1912), and since the anal brushes are extruded during courtship (e.g. Sevastopulo & Carpenter, 1944; Poulton, 1915), it is generally assumed that the sexual spots secrete some aphrodisiacal material which is transferred to the anal brushes for use during the courtship of the female. Differences in the observed courtship behaviour of various danaids suggest that the significance of the anal brushes may differ from species to species.

Although many males of *D. chrysippus* were kept under observation in the flight cage in Ghana, none was observed to insert the anal brushes into the pockets of the sexual spots. As an experiment, a slow-drying ink, such as is used in recording instruments, was inserted into the wing-pockets of three males, and in each case the brushes became coloured with the ink.

However, when the wings are folded over the back of the butterfly, the pockets are closely approximated to the end of the abdomen, and it is possible that the brushes were coloured by direct contact with the end of the abdomen, the latter having acquired the ink by direct contact with the wing pockets.

As noted above, the males of *D. chrysippus* rapidly become habituated to the presence of the females. Thus eight males were kept in the flight cage for several days in the absence of females. During this period they showed little reaction to each other's presence except when preparing to roost. On the sixth day six virgin females were liberated in the cage, and the males immediately commenced courting them. Two or three groups of males became associated with separate females, the males flying above the females and dropping down to strike the heads of the latter with the anal brushes. If the female was lost during the confusion of this multiple courtship, the males continued to buffet each other for a short while. The group would soon break up, however, to form again when another female was discovered. After about fifteen minutes of such activity the males showed signs of an increasing reluctance to court, and after an hour the males were apparently habituated to the presence of the females and no longer showed any tendency to court. Two pairs of butterflies copulated during the initial burst of activity and were removed from the cage. Three of the remaining females copulated at widely separated times during the following week. Throughout this period the males generally showed little interest in the females, and there was some indication, in fact, that the females tended to take the initiative in courtship since they were frequently observed to fly up underneath and to the fore of passing males.

The flight of the female *D. chrysippus* is normally slow and unhurried. In the few successful courtships observed, this slow flight was replaced by a rapid rather jerky flight consisting of a series of short dashes. The male flew above the female, and each time opportunity offered he dipped down to strike the front part of the female with his anal brushes. In a short time the female settled on a leaf or the side of the cage and the male settled beside her, facing the same direction. Copulation was effected by a flexion of the male abdomen in a forward direction. Any further movement on the part of the paired butterflies was effected by the male, which appears to be the active partner in this species.

The most satisfactory observations on the extrusion of the anal brushes were made on free-living males. During part of the year at Achimota (Ghana) *D. chrysippus* is a comparatively scarce butterfly. This period coincides with the period of greatest abundance of *H. missippus*, and on two or three occasions during the work on *H. misippus*, the female test insects were approached and courted by *D. chrysippus* males. Presumably these males had acquired an unusually strong tendency to court as a result of the scarcity of the females. So completely were the males involved in courting the dead test insects that it was possible to hold the latter in the hand and observe the actions of the male at close quarters. The males hovered about four inches above the dead female, and continually dipped down onto the front part of the female, rising again immediately afterwards. At the lowest point of each "dip" the male abdomen was flexed forward and the anal brushes were momentarily extruded to strike the female. The whole process was carried out extremely rapidly, the male dipping at the female about once a second—this made observation of the finer details of the process impossible.

Papilio dardanus

The courtship of *P. dardanus* was essentially similar to that of *P. demodocus*. In both species the male flew up underneath the flying female so that the latter was probably forced to settle on the male's thorax as a result of his interference with her flight. The male then attempted to flutter gently to the ground carrying the female with him. "Unwilling" females were able to escape during this descent. Six virgin females of *P. dardanus* mated the first morning that they were liberated into the flight cage, indicating that the cage was sufficiently large for the courtship flight of this comparatively large butterfly.

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TEMPERATURE PREFERENCE DETERMINATIONS USING *Tribolium*

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Introduction

In stored-products entomology an understanding of insect temperature preference behaviour has become essential. Within the fabric of a building, a bag of grain, a stack of bags, or in the bulk of a silo, there is a maze of temperature gradients. If insects react to these gradients the results are important in comprehending population dynamics, and in applying control.

A major work on insect temperature preference was that by Deal (1941), and the literature prior to 1941 is reviewed by him. He employed a number of species in his preference determinations. Using *Tribolium confusum* Duval, he determined its temperature preference when in an empty trough, and also while in bran, (a satisfactory food medium). The latter aspect of his work was original but relatively cursory. The intent in the present work was to enlarge upon Deal's work, using the flour beetles *Tribolium castaneum* Herbst. and *T. confusum*.

A temperature gradient in the field always has a coexistent gradient of air relative humidity. To separate the temperature and R.H. gradients in the laboratory is artificial, yet necessary if we are to understand the relative importance of these two factors.

Roth & Willis (1950, 1951) experimenting with *Tribolium* determined R.H. preferences when the test insects were given a choice of alternate relative humidities at a constant temperature. *T. confusum* and *T. castaneum* showed a preference for the lower R.H. when the alternate values were separated by 15 per cent. R.H. or more. The reactions could be reversed by a prior starvation and/or desiccation of the test insects. Between the R.H. values 40 per cent. and 45 per cent., 45 per cent., and 50 per cent. and 50 per cent. and 55 per cent. they showed no preference reaction. In light of this it seemed important to establish a temperature gradient combined with a very slight R.H. gradient in the region of 50 per cent. R.H.

Much time was spent obtaining a temperature gradient in a flour mixture which was relatively free of an R.H. gradient. When this was accomplished, comparisons were made between the temperature preferences of *T. castaneum* and *T. confusum* which had been cultured at 27°C. Both species were also held at a conditioning temperature of 20°C., and their behaviour on the gradient compared. Other minor points relative to their preference behaviour were investigated.

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Apparatus and Method

The apparatus in which the temperature gradient was set up was a rectangular cast aluminium trough with wall and floor about 1 cm. thick, and with internal dimensions of 8·40 cm. x 3·8 cm. x 1·6 cm. deep. It had an inner perspex and outer wooden cover, through which five thermometers were inserted via corks into the contained flour mixture (less than 1 cm. deep). Nine corked holes on the side of the trough gave further access which facilitated R.H. determinations. By the use of two lamps level with one end and ice beneath the other a very constant gradient with a range of 17·0°C. (30·5° to 13·5°C.) was maintained. The steepness of the gradient was 1°C. in 5 cm.

Using an empty trough results in an inseparable inverse R.H. gradient. Several workers, Nieschulz (1933), and Gunn (1934), partially succeeded in overcoming this limitation in their apparatus. Most workers overcame the problem by simply ignoring its existence. I decided upon employing the moisture sorbing nature of the food medium which I used in the trough as a means of R.H. control.

A number of workers have determined equilibrium curves for grain moisture content—air R.H. In an open system (where nearby limitless quantities of air of a uniform R.H. are available, or where excess moisture is added or removed by chemical solutions) the percentage moisture content of the grain is determined only by air R.H. The moisture content (M.C.) is nearly unaffected by those temperature changes which are not accompanied by R.H. changes, (Gay, 1946). In a closed system such as the trough I used, as simple a relationship does not always prevail.

Rough calculations indicate that a closed system, containing flour of a moderate M.C.

exposed to a temperature increase of. 20°C., in the region of 10° to 30°C., will react thus:

(*a*) When the volume of air enclosed is 200 to 400 times the volume of the grain, the grain M.C.—air R.H. equilibrium is practically unaltered.

(*b*) When the volume of air enclosed is approximately 500 times or greater than the grain volume, the grain M.C. and air R.H. are held comparatively lower, because of the increase in the air's initially large potential for water retention.

(*c*) When the volume of air is less than approximately 100 times the volume of the grain, the point of equilibrium is increased, because the moisture released by the grain is far in excess of that which the air can retain.

Most measures of grain greater than a few grams are of necessity enclosed with volumes of air much less than 100 times the grain volume. Feasible examples of the closeting of grain in storage, or in the laboratory, result therefore in the level of the R.H.—M.C. equilibrium being raised when the temperature is increased.

With a capacitance resistance hygrometer, the Jason Hygrometer, (Cutting, Jason & Wood, 1955, and Underwood & Houslip, 1955), it was possible to take readings of R.H. in the small space over the flour, via the nine holes in the side of the trough. By using small spatulate elements it was possible also to take reliable air R.H. readings actually in the flour. When the trough containing flour with a 10 to 12 per cent. M.C. was heated at one end there occurred a steep R.H. gradient. The slope of the gradient was of the same sign as the temperature gradient, but within a few days the gradient levelled (due to moisture translocation), and then reversed its slope. As expected, the R.H. gradient was initially of the opposite slope to that gradient which would exist in an empty trough heated in a similar manner. It was concluded that if the volume of the air over the flour was increased to ten times that of the flour, and if the M.C. of the flour was near 11 per cent. a nearly ideal levelling of the gradient could be obtained in a matter of hours. The resultant lack of a R.H. gradient would be maintained for the few hours necessary to complete an experiment on temperature preference.

The ratio of air to flour volume that could easily be obtained was only 2-1, so that the findings could not be fully employed. The ratio of air to flour volume was kept as high as possible and a flour mixture with a M.C. of about 11 per cent. was used. The result was not far from the ideal; the R.H. midway along the trough was 50 per cent., and the gradient range was only occasionally in excess of 20 per cent. R.H. For those experiments where a R.H. gradient was to be avoided flour mixtures of varying M.C. (10 per cent. to 13 per cent.) were distributed in the trough. Flour with the lowest M.C. was placed at the end which was to be heated. After the temperature gradient had been maintained for several hours, the R.H. gradient was negligible.

Experiments in which there were R.H. gradients of a positive slope, or a negative slope, and with no slope were performed. *Tribolium* (100 per test) were injected into the centre of the trough onto the surface of the flour. The temperature gradient was maintained for four hours. The covers were lifted, and the flour quickly separated by movable partitions into five equal sections, then removed to petri dishes. The beetles were counted and recorded as showing a preference for one of the sections. The temperature ranges for each of the five sections are shown on Table I.

In all experiments the *Tribolium* distributed themselves without regard to the R.H. gradients, therefore no details of the R.H. gradients used in individual runs will be included here. In the majority of runs the R.H. gradient corresponding to the temperature gradient of 30.5° to 13.5°C was 60 per cent. to 40 per cent R.H.

An initial series of experiments showed that when groups of 100 *Tribolium* were left in the trough, on the temperature gradient, for 1, 3, 4, or 5 hours respectively, the resulting distributions were not significantly different (X^2, ·05 per cent. level). The period of a test was set at four hours. Distributions were the same when less than 100, or over 300 adults were used. For ease of handling about 100 *Tribolium* were used in each test.

Results

Using *T. castaneum* which had been reared at 27°C. and 72 per cent. R.H. several series of experiments using different age groups were completed. Adults of 1 to 3 weeks showed an unstable, yet definite reaction to the warm end of the trough. Tests using a total of about 2,000 adults 3 to 8 weeks old gave easily repeatable results. Results from only one group (the N-series) need be presented here.

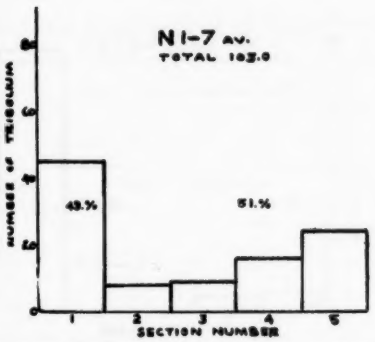

Fig. 1. Average distribution of *T. castaneum* from 27°C. *Note.*—In this and the following seven illustrations the respective mean temperatures of Sections 1 to 5 are 28·0°, 24·7°, 21·5°, 18·3° and 15·0°C. The percentage values indicate the proportion of beetles occurring above and below 25°C.

Table I. The N-series—4-week Old *T. castaneum* from 27°C. and 72 per cent. R.H.

	Section no. and temp. ranges					
	1 30·5°– 26·3°	2 26·3°– 23·0°	3 23·0°– 19·8°	4 19·8°– 16·6°	5 16·6°– 13·5°	
Run no.	Number of *Tribolium*					Total
N1	59	10	10	9	15	103
N2	33	6	14	22	27	102
N3	56	8	8	14	20	106
N4	45	7	5	23	27	107
N5	51	7	11	11	24	104
N6	40	12	6	18	26	102
N7	32	5	9	15	35	96
N1–7av.	45·2	7·9	9·0	16·0	24·9	103·0

Table II. A Statistical Comparison of Consecutive Tests

X^2 comparison	
N1 & N2 – P<·01	N1 & N3 – P>·05
N2 & N3 – P>·05	N1 & N4 – P>·05
N3 & N4 – P>·20	
N4 & N5 – P>·20	
N5 & N6 – P>·20	
N6 & N7 – P>·20	

It may be asked whether the beetles found in Sections 1 and 5 would be found at higher and lower temperatures if these were available. However, the use of a more extensive range showed that very few beetles were ever found at temperatures above 29°C. This observation applies to all of the *Tribolium* which were used. Often at the termination of a test, groups of, forty to eighty beetles were observed clumped on the surface in a region only about 1 cm. long, at 27° to 28°C. The limit of distribution at the cooler end was not so marked, yet rarely were many below 14°C. Those individuals showing a preference for a temperature lower than that of the trough are of little interest, for as Deal (1941) noted, in the neighbourhood of 10°C. "cold trapping" occurred. The suggestion that the distribution could be due in part to the less rapid movement of *Tribolium* in the cooler region, and further that what has been taken here as a preference might be an avoidance reaction was investigated in a series of two tests. In the usual test *Tribolium* were injected into the centre of the trough through one of the holes on the side. *T. castaneum* similar to those used in the B-series (Table III) of tests were injected into the trough in the 14° to 15°C. region. Four hours later they had moved to a distribution not significantly different (·05 per cent. level) from the B-series average distribution. Next *T. castaneum* were injected into the trough in a temperature region above 28°C. They likewise took up a distribution not significantly different from the B-series average. These similarities could not have occurred if there had been an avoidance reaction toward a temperature which fell between 28°C. and 15°C., or if an extreme temperature had affected their reaction adversely. After preliminary experiments it was decided to use a temperature gradient with only a 17° range so that the chance of adverse effects on behaviour due to extreme temperatures not normally experienced would be minimised. Further it was found that the smaller the range the easier it was to maintain a non-fluctuating gradient.

Several runs using *T. castaneum* from 27°C., over three months old, showed the same bimodal distribution.

T. castaneum which had been kept at 20°C. and 50 per cent. R.H. for several weeks after reaching maturity gave equally repeatable results. Table III and Fig. 2. The table of X^2 need not be included; no two consecutive runs showed a significant difference at the ·05 per cent. level.

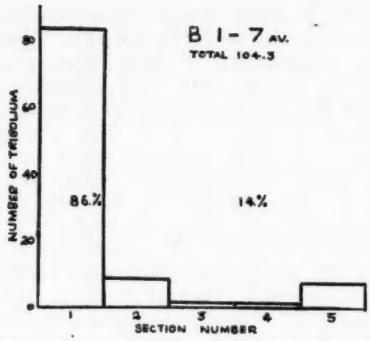

Fig. 2. Average distribution of *T. castaneum* from 20°C.

Table III. The B-series—Mature *T. castaneum* from 20°C. and 50 per cent. R.H.

	Section no. and mean temp.					
	1 28·0°	2 24·7°	3 21·5°	4 18·3°	5 15·0°	
Run no.	Number of *Tribolium*					Total
B1	79	9	5	2	5	100
B2	80	8	4	5	11	108
B3	75	15	3	2	9	104
B4	79	17	0	2	11	109
B5	90	8	0	0	4	102
B6	92	1	1	0	12	106
B7	89	6	1	3	2	101
B1–7av.	83·4	9·0	2·0	2·0	7·9	104·3

A group of runs using *T. castaneum* from 20°C. which were over six months old (six months at 20°C.) gave a distribution not significantly different to the B1-7 av. ($P > \cdot 05$).

Using *T. confusum* from 27°C. and 72 per cent. R.H. which were five weeks old the H-series was obtained. Table IV, and Fig. 3. The H1 to H5 runs as a group have $P > \cdot 20$.

The results with *T. confusum* are in good agreement with work done by Bodenheimer & Schenkin (1928), and Deal (1941).

T. confusum which, prior to testing, had been kept at 20°C. and 50 per cent. R.H. for three weeks of their nine weeks of adult life gave a less consistent series of runs (the K-series). Table V, and Fig. 4. The runs are not such good replicates as most of the other series, yet their average can reasonably be considered as typical for *T. confusum* adapted to a temperature of 20°C.

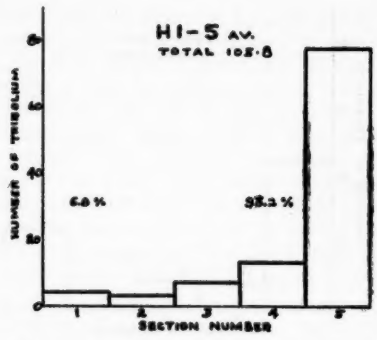

Fig. 3. Average distribution of *T. confusum* from 27°C.

Table IV. The H-series—4-6-weeks-old *T. confusum* from 27°C. and 72 per cent. R.H.

	Section no. and mean temp.					
	1 28·0°	2 24·7°	3 21·5°	4 18°3·	5 15·0°	
Run no.	Number of *Tribolium*					Total
H1	5	1	5	13	85	109
H2	5	4	9	11	86	115
H3	6	3	4	19	69	101
H4	1	4	5	14	79	103
H5	7	6	12	8	68	101
H1–5av.	4·8	3·6	7·0	13·0	77·4	105·8

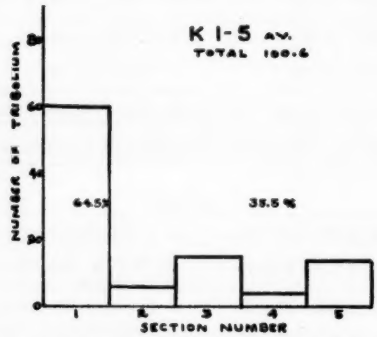

Fig. 4. Average distribution of *T. confusum* from 20°C.

The third peak in Fig. 4 (the 21·5°C. region) should possibly be disregarded as repeated observations suggested that it was caused by the beetles clumping at a worn cork in that region.

Table V. The K-series—9-week-old *T. confusum* from 20°C. and 50 per cent. R.H.

	Section no. and mean temp.					
	1 28·0°	2 24·7°	3 21·5°	4 18·3°	5 15·0°	
Run no.	Number of *Tribolium*					Total
K1	64	5	17	4	9	99
K2	54	9	27	5	3	98
K3	62	0	16	4	22	104
K4	68	12	9	4	6	99
K5	56	4	9	5	30	104
K1–5av.	60·8	6·0	15·4	4·4	14·0	100·6

When the temperature preference reaction is relaxed a thigmotactic reaction apparently becomes more marked.

When *T. castaneum* were moved from 27° to an environment of 20°C., the typical 20°C. reaction was not attained until after one week. The distributions in the first week were erratic, but there appeared to be an initial intensification of the 27°C. reaction. The transition of behaviour when *T. castaneum* were moved from 20° back to 27°C. also occurred after about one week.

T. confusum moved from 27° to 20°C. similarly showed a transition of reaction which took over one week to become established (I-series). Figs. 5 to 8, representative of this transition are included, for they elucidate the interpretation which will follow, of the *Tribolium* temperature preference reaction. I1, I2, I3, I4 are tests done 1, 2, 4, and 16 days after the adults had been moved to 20°C.

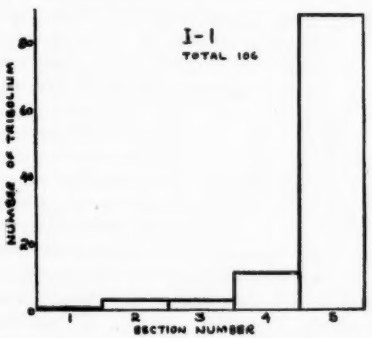

Fig. 5. *T. confusum* distribution one day after being moved from 27°C. to 20°C.

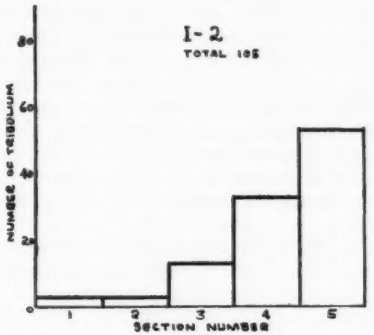

Fig. 6. *T. confusum* distribution two days after being moved from 27° to 20°C.

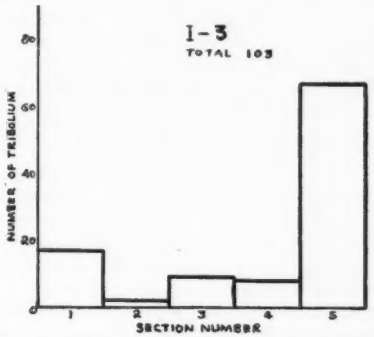

Fig. 7. *T. confusum* distribution four days after being moved from 27° to 20°C.

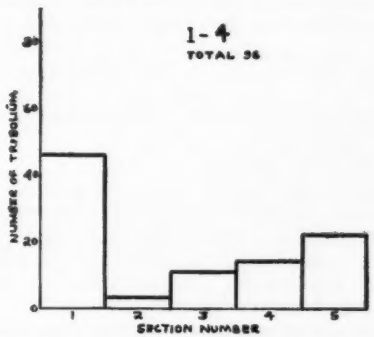

Fig. 8. *T. confusum* distribution sixteen days after being moved from 27° to 20°C.

Discussion

The reactions of both species appear to turn at 26°-24°C. Those reacting to a temperature higher than 25°C. have a sharply peaked distribution, the majority collecting very near 28°C. Those reacting to a temperature below the turning point of 25° show a preference for 14°C., but their distribution is skewed towards the warmer region. This balanced relationship of the warm end and cold end preferences is fairly apparent in the two groups of *T. castaneum*. It is best illustrated for *T. confusum* by the transitional I-series.

Both species showed their most intense warm end reaction when they had been formerly kept at a lower temperature. Regardless of which temperature adults were held at, *T. castaneum* showed a more intense warm end reaction. That is, both species showed the same bimodal temperature preference, but the intensity of reaction towards the higher of the preferred temperatures was greater for *T. castaneum*. The interrelation of the preferences of the two species is seen by studying the graphs of the four illustrative groups in the following order:

T. castaneum from 20° (B) 86.0% (Fig. 2)
T. confusum from 20° (K) 64.5% (Fig. 4)
T. castaneum from 27° (N) 49.0% (Fig. 1)
T. confusum from 27° (H) 6.8% (Fig. 3)

The percentage values noted are those of the totals distributed above a temperature of 25°C. (the turning point). In computing this percentage two-thirds of those in section two are considered to be from a temperature above 25°C.

That the two-peaked reaction was not due to strains within the species was shown by a further group of experiments. From tests using several hundred *T. castaneum* from 27°, those showing the warm end preference were reintroduced for a second four-hour test. Their preference for the warm end was greater than normal, but of more importance was that in four hours 30 per cent. of the reintroduced adults had reverted to a cold end preference. Similarly, adults taken from the two coldest sections showed within four hours a 27 per cent. swing to a preference for 28°C. Many hundreds of *T. castaneum* collected from the cold end of the trough were grouped, and when tested two weeks after their initial segregation they showed a completely normal (N-series) distribution. The preference for 28° or for 14°C. is completely transitory.

It would be of interest to determine the temperature reactions of populations of other species of *Tribolium*. Species differences in intensity of temperature preference may well have been a factor in speciation.

The difference in temperature reaction between *T. castaneum* and *T. confusum* must be a strong factor in determining the present geographical species distribution. Good (1936) observed that "records in the United States of America indicate temperature has quite an effect on distribution. *T. castaneum* is essentially an insect of warm climates and although sometimes recorded from Canada and other Northern countries, it is evidently not a permanent resident north of the fortieth parallel in Eastern United States of America except in heated buildings. *T. confusum* on the other hand, is more frequently found in the Northern part of the United States of America than in the Southern part. From 37° to 40° north both species occur commonly, while south of 37° *confusum* gradually becomes less common and in the Gulf States is largely replaced by *castaneum*". On a more limited scale; it has been observed in Kenya that *T. confusum* occurs appreciably only in the Highlands, whereas *T. castaneum* occurs in vast numbers in the lower, warmer regions of Kenya.

Conclusions

The temperature preference reactions of *T. castaneum* and *T. confusum* are so changeable that it is best to express preference as a population characteristic. The warm end preference expressed as a percentage of total distribution can be interpreted as the percentage of the cycle-time that the population spends at 28°C. The remaining period of the cycle is spent in the region of 14°C. The intensity of reaction towards 28° or 14°C. is dependent upon the environmental temperature at which the population was previously kept; a colder environment initiates a more intense warm end reaction. A *T. castaneum* population from a warm environment has a markedly more intense reaction towards 28°C. than *T. confusum* (46 per cent. as against 7 per cent.). *T. castaneum* has therefore an advantage over a *T. confusum* population from the same environment, for production of ova is greatest at temperatures above 25°C.

The most obvious conclusion is the necessity for further investigation. The cycle-time and its possible variations have not been definitely determined. The effect, if any, of previous environment R.H. has not been analysed. The behaviour of *Tribolium* kept initially at other

constant environments, and on a gradient environment for several weeks, has not been investigated. Larvae have not been experimented with to date.

Though the analysis of this aspect was not a thorough one, certain preliminary conclusions can be drawn. Since a population of *T. castaneum* from 27° has at one instant about 50 per cent. of its individuals at 28°C., and since such a preference is transitional, any one individual must spend 50 per cent. of its time at 28°C. Furthermore, since 30 per cent. of the individuals at 28° moved to 14° within four hours, all individuals should spend about 12 hours at 28° and then a similar time at 14°C.

Experiments are lacking, but if for illustrative purposes we consider the total time of the *T. confusum* behaviour cycle to be also about 24 hours, then the time spent at 28° by an individual conditioned to a 27° environment would be less than two hours; percentage warm end distribution of the population is 7 per cent. and 7 per cent. of 24 hours is less than two hours.

Such a cycle of behaviour must be linked with production of ova, since in the vicinity of 20°C. production ceases, (Dick, 1937). It was therefore determined if different preference behaviours were shown by males and females. The male was found to have only a slightly greater preference for the warm end, and the female a greater preference for 14°C. It can be assumed that an ovarian cycle is not regulating this cycle, though temperature does affect production of ova.

Eggs are only laid in appreciable numbers while the female is at a temperature greater than 25°C., thus percentage warm-end preference is a rough measure of that population's potential for reproduction—independent of fecundity, fertility, times of development, etc. In an environment where the average temperature is 27°C. a *T. castaneum* population has the advantage over *T. confusum* (46 per cent. as against 7 per cent.), since its stronger preference for the warm end signifies a greater potential for reproduction. In an environment averaging near 20°C., *T. castaneum* also has a slight theoretical advantage (86 per cent. as against 64 per cent.), but other factors might mask this advantage in determining reproduction and survival.

The cycle of movement on a gradient might also serve to maintain a high rate of oviposition. Dick (1937) showed that female *T. confusum* moved to 18° then back to 28°C., had their production of ova stimulated. In grain stores the cyclic movement must also serve to disperse *Tribolium* from centres where the temperatures are dangerously high.

In addition to an indication of the need for more exact and extensive temperature preference work; the question of inter-species population competition needs further exploring, the effects of temperature behaviour upon oviposition could be a rewarding work, and there is a need for knowledge of sensory mechanisms, and of the physiology underlying the cyclic temperature behaviour.

Acknowledgments

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SYNCHRONOUS CLAW-WAVING OF FIDDLER CRABS

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Introduction

A recent study was made of the ecology and behaviour of the five species of *Uca* crab, which occupy the mangrove swamps of Inhaca Island, off the coast of Mozambique. The species studied were *U. annulipes*, *U. inversa*, *U. chlorophthalmus*, *U. marionis* and *U. urvillei*. The crabs were observed during several seasons, extending over a period of about a year, that is, from April, 1954, to May, 1955. One of the aspects studied was the characteristic waving-movement of the major cheliped of male crabs, a phenomenon generally referred to as "claw-waving" or "claw-beckoning."

Various workers on *Uca* have already expressed their views on the function served by the claw-waving of the male. Verwey (1930), for example, claims that claw-waving is used exclusively as a means of threat, to warn intruders off the territory of the beckoning individual. Crane (1941), however, while admitting that claw-waving is used as a means of territorial defence and, thus, as a means of delimiting the territory of each individual, asserts nevertheless that claw-waving plays a major role in courtship, it being the chief method used to attract individuals of the opposite sex. Crane further points out that this latter function is especially noticeable in those species in which waving is limited to the reproductive season. Peters (1955), while studying the variations in the methods of claw-waving shown by certain species of *Uca* and *Minuca*, found that the method of waving varies from one species to another, particularly in the duration of the movements involved. Within any one of his species, however, the method of beckoning appears remarkably stereotyped. Peters asserts that claw-waving in *Uca* crabs is chiefly a means of territorial defence, because the individuals occur generally in very dense populations and, not only do they spend a long period of every day out of their burrows, feeding, but they have an unobstructed view of one another on the feeding-grounds. Altevogt (1957), on the other hand, asserts that, in the three *Uca* species studied by him, claw-waving has no function as a means of delimiting territories, but serves only in attracting females during the breeding-season. He found that there was, in fact, very little claw-waving taking place during the normal feeding and burrow-digging periods of these species.

The male crabs of the five Inhaca species showed claw-waving both as a means of threat, to a varying degree throughout the year, and—with the exception of *U. inversa*, in which no real courtship-display was ever observed—as a means of attracting females, only during the breeding-season. It should be noted, in passing, that the breeding-seasons of the five species do not quite coincide with each other, some of the species starting to show courtship behaviour earlier than others, As a general rule, aggressive behaviour towards intruders was greater during the courting and breeding-season of the species than during the rest of the year, and actual fighting—involving the gripping of one another's claws—was at all times relatively rare as compared with threat. Crane (1941) found that, in the *Uca* species of Panama, threat-display only very rarely preceded a duel, but, in the Inhaca species, actual fighting took place only on the relatively rare occasions when threat-display had failed. Tinbergen (1951) has noted that fighting in animals usually consists of threatening or bluff, and this is certainly the case in the *Uca* species of Inhaca.

Claw-waving is used both as a means of threat and as a means of courtship-display, but the method used was found to vary from species to species, while remaining very constant within any one species. In this way, the Inhaca species resemble the El Salvador species of Peters (1955). Generally speaking, the male *Uca* crabs of Inhaca use almost the same basic movement of the major cheliped, whether such a male is threatening off some other individual from his territory, or courting a female crab. In most species, however, when a male is trying to attract the attention of a passing female, the display-movement used is generally faster, more definite, and of a somewhat higher intensity than that observed during threat-display. It was found, too, that in *U. annulipes*, for example, a crab engaged in threat-display may jerk about,

but to a lesser degree than in courtship. Moreover, during threat, he tends to remain more or less in one spot while waving his cheliped, and nearly always stays in the near vicinity of his burrow. Thus, the running about and the jerking movements of the body from side to side are generally associated with the attracting of a female's attention during courtship, and not so much with threat. Unlike Altevogt's species, which nevertheless also include *U. annulipes*, the Inhaca species certainly show threat and a certain amount of actual fighting, chiefly centring around the ownership of burrows, during normal feeding and burrow-digging periods.

In addition to the usual claw-waving associated with threat and courtship, however, various modifications of the phenomenon of claw-waving were also shown by individuals of four of the five Inhaca species. In each case, this special type of claw-waving appeared to serve no particular purpose. The most striking, and certainly the commonest of these variations was what can best be described as a widespread "synchronous claw-waving", shown only by males of *U. annulipes*.

Synchronous Claw-waving in *U. annulipes*

Synchronous claw-waving—a peculiar type of rhythmic claw-waving, involving small groups of male individuals—was first noticed during February, 1955, at two of the Inhaca mangrove swamps, where *U. annulipes* individuals abound. This type of concerted waving appeared to be more or less at its peak during February, when it was mid-summer, for every *U. annulipes* population in both the swamps seemed to have a few groups of synchronous claw-wavers. During another visit, towards the end of April and beginning of May, when the weather was cooler, synchronous claw-waving was again observed at both these swamps, but to a lesser extent. Not only was the number of synchronising groups noticed in any one population considerably fewer, but the synchronous waving itself was, generally speaking, somewhat less intense. As a result of this, most of the observations on synchronous claw-waving were recorded during February.

Apart from being at its maximum during the warmer months of the year, synchronous claw-waving showed also a daily peak, which was reached during the hottest part of the day, the waving being at its most intense during these hours. Early in the morning and in the late afternoon, there were fewer groups of synchronous wavers to be seen, and most of the claw-waving taking place at these times was performed by scattered males independently of one another. There was always a greater number of waving groups in sunlit areas than in the shade where, as a general rule, the individuals were definitely rather sluggish, being far less active than those exposed to the sun.

Synchronous claw-waving generally seemed to start when one or rarely two individuals would begin to wave with their major chelipeds, occasionally as a reaction to a passing female but nearly always for no apparent reason. Almost immediately, one male after another in the vicinity of the beckoning individual or individuals would generally begin to wave his major cheliped until there was a small group of individuals, moving automatically in unison, the movements of their bodies and chelipeds being synchronised to a remarkable degree. The individuals in each group appeared to be in some way lulled by the rhythmic movements of their fellows, for they generally continued waving thus for an average of about ten to fifteen minutes. There were usually about five to seven crabs in a group, all facing the same way or in different directions, some even standing back to back with one another. Very occasionally, when a particular female happened to be the "trigger" setting off the claw-waving mechanism in the first male individual, she would gradually become more or less surrounded by a ring of males, waving synchronously. Such claw-waving however, would invariably continue long after the female had moved away, and new individuals that had never even seen the female responsible might join the group. Frequently, there were as many as ten small groups of synchronous wavers in a small area, and these groups would usually overlap one another to a certain extent. For example, a particular male involved in the synchronised waving of one group might suddenly, and for no apparent reason, become involved in the synchronised waving of a neighbouring group. Moreover, adjacent groups of synchronous wavers might gradually merge together to form a larger group, in which all the individuals would eventually begin to wave their chelipeds in unison.

The individuals did not appear to feed whilst they were engaged in synchronous waving, but an individual in a group might gradually stop waving, and possibly, move a short distance away, in order to feed, often quite busily. Should such an individual by any chance move into the

midst of a neighbouring group of synchronous wavers, however, he would generally stop feeding almost at once and automatically join in the waving of this group. The fact that the individuals comprising a group moved about and changed their group from time to time was another way in which overlapping of the groups would take place.

Each individual, then, would tend to alternate spells of synchronous claw-waving with bouts of feeding, or such a crab might begin to show independent claw-waving, usually to threaten other males but occasionally, in February anyway, to attract the attention of passing females.

As gradually as it began, synchronous claw-waving would end. Just as one individual after another gradually took up the movement until a group was formed, so one individual after another would gradually stop waving, again for no apparent reason. Although the majority of synchronous claw-wavers were adult, some rather small young forms were noticed in many of the groups.

The Movements Involved in Synchronous Waving

The claw-waving movements of each individual in a synchronising group were found to be essentially similar to the normal beckoning movements used by a male when threatening another male or when attracting the attention of a passing female. The movements involved, however, seemed to be even more exaggerated than those used in courtship-display which, in its turn, as has already been pointed out, involves movements which are not only faster and more jerky than those of threat-display, but which are also more clearly defined and of a higher intensity.

The movement of each individual in the group was seen to start originally with the position of rest: that is, the ambulatories were slightly bent and the major cheliped was held bent and in the normal horizontal plane, with the claw itself pointing slightly forward. The cheliped would then be extended and stretched out sideways to the very fullest extent and, with the cheliped held in this position, the crab would give a pronounced jerk or jump, reminiscent of courtship-display, generally moving a short distance to one side but, very occasionally, landing on the same spot. Next, while raising himself on to the tips of his now straightened ambulatories and lifting his minor cheliped, the individual would raise his major cheliped as high as possible, so that the claw was pointing upward, then swing it first down and in towards his body and finally out to the side again, in a smooth, continuous movement.

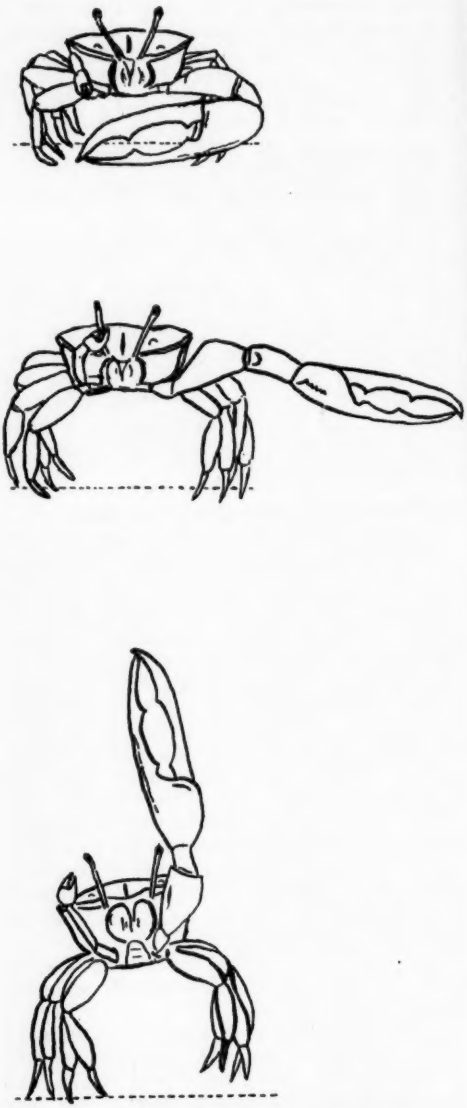

Fig. 1. The main positions of the chelipeds and ambulatories during synchronous claw-waving of *U. annulipes*.

As the major cheliped was raised to its highest point, a few of the ambulatories on the side of the major cheliped might even be lifted momentarily from the ground. As the major cheliped was lowered and restored to the position out at the side of the individual, the minor cheliped would also be somewhat lowered, and the ambulatories bent slightly once again. The main positions of the major cheliped in relation to the body are illustrated in Fig. 1.

Following each beckoning-movement, there was a definite pause of about a second or two, after which the crab would generally jerk once again, this time usually to the side opposite but occasionally to the same side as previously, and then the whole claw-beckoning movement would be repeated. The individuals in a synchronising group would generally keep nearly perfect time with one another, but occasionally the beckoning movements of individuals would tend to overlap one another very slightly, one individual starting to move his major cheliped before another which, in his turn, would start the waving-movement before yet another individual, and so on. On the whole, too, the crabs would all jerk at approximately the same instant, and they would generally all jerk to the same side, whether or not they were all facing in the same direction.

Discussion

The synchronous claw-waving shown by males of *U. annulipes* is obviously a highly specialised form of beckoning, the function of which is not clear. It certainly does not form part of either the threat- or courtship-pattern, although the first male of a group sometimes begins his initial waving as a reaction to a passing female.

Since it is a phenomenon which appears to be correlated with temperature, synchronous claw-waving can probably best be described as a physical expression of abundant energy in a sun-loving genus. The fact that this energy finds expression in this particular way in only one of the five Inhaca species can perhaps best be explained by the fact that *U. annulipes* individuals spend the longest daily period of all five *Uca* species feeding, out of their burrows and exposed to the heat of the sun.

Summary

1. An ecological and behavioural study was made of the five *Uca* species of Inhaca Island.

2. In addition to the claw-waving shown by males as a threat-display or as part of courtship behaviour, various modifications of the phenomenon of claw-waving were also noticed. The most widespread of these modifications was a type of synchronous claw-waving, shown only by males of *U. annulipes*.

3. Synchronous claw-waving is a form of concerted waving by small groups of individuals.

4. The movements involved in synchronous claw-waving are described in detail.

5. Synchronous claw-waving showed both a seasonal and a diurnal peak, and thus has a definite connection with temperature.

6. This highly specialised form of claw-waving is probably due to the abundant energy of the *U. annulipes* individuals, which spend the most time of all the species above-ground, feeding.

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PROCEEDINGS OF THE ASSOCIATION FOR THE STUDY OF ANIMAL BEHAVIOUR

An Ordinary Meeting of the Association was held on 3rd January, 1958, in the Department of Psychology, Birkbeck College, London, by kind permission of Professor C. A. Mace. The President, Dr. Tinbergen, was in the Chair, and the following papers were read.

POLAR LOCOMOTION AND EXPERIMENTAL "NEUROSIS" IN THE AMOEBA

By R. J. GOLDACRE
London

Experiments on the behaviour of *Amoeba proteus* in capillary tubes and in circular tracks reveal that it does not reverse but has a permanent polar organisation and a permanent rear contracting end. By micromanipulation it was shown that this polar organisation is maintained by a mechano-chemical feedback process, in which the area of contact of cell membrane and plasmagel is automatically regulated.

While in the free amoeba this results in homeostasis, under certain experimental conditions there is a dramatic switch-over to oscillatory behaviour. One method of inducing oscillatory behaviour is superficially analogous to that used for inducing neurosis in rats. This disorder in the amoeba (from which it recovers when rescued) may be the simplest form of behavioural disorder in animals.

VISUAL PERCEPTION AND BEHAVIOUR IN THE DESERT LOCUST

By G. K. WALLACE
Department of Psychology, University of Reading

Locust nymphs show spontaneous attraction to objects in the visual environment. This paper was concerned with certain of the properties which make such objects attractive and in particular with object shape and distance from the insect. The experiments reported here suggest that these two properties may be very similar in their stimulatory effects. The experiments fall into two main groups.

1. The relative attractiveness of different shapes was measured by presenting these as two-dimensional black areas on a white background and counting the number of visits to each type of shape. Pairs of shapes were contrasted in this way. It was found that there was a distinct attraction to the edge of a shape, that vertical edges were preferred to oblique or horizontal edges and that straight vertical edges were preferred to wavy or serrated edges. In the absence of vertical edges the figure with the more complex contour was preferred.

Most of these results can be explained on the basis that the insects are attracted to the shape whose contour produces the greater number of stimulus changes per unit time in the retina. Superimposed on this may be a preference for certain patterns of stimulation.

2. From time to time locust nymphs show a side-to-side swaying motion of the anterior part of the body and the head. This is called "peering" (Kennedy, 1945). Experiments showed that this was a visual scanning movement and concerned, amongst other things, with the estimation of distance. Two-choice jumping experiments showed that of two objects at different distances the nearer was preferred. The insects jumped on the objects accurately. The ability to choose the nearer object did not depend on binocular vision nor on the angle subtended by the object. Peering always preceded the choice of object and the actual jump on to the object. When a single object was presented and moved in the opposite direction to the head movement whenever the insect peered the insect jumped short of the object.

The results supported the hypothesis that the insect estimates distance by measuring the move-

ment of the object image over the eye produced by the peering motion.

It was suggested that the similarity between the properties object shape and distance was that both influenced the number of stimulus changes per unit time in the retina. Preference was shown for a near object because its contours moved a great distance over the retina and produced a large number of such changes. This was also the basis of attraction to certain shapes.

SOME FACTORS CONTROLLING THE EVOLUTIONARY CHANGE OF SOCIAL DISPLAY

By N. TINBERGEN
Oxford

This paper will be published in full elsewhere.

A Joint Meeting with the Experimental Psychology Group was held at Cambridge on 26th and 27th March, 1958. The theme of the discussion was "Discriminating Mechanisms" and the following papers, abstracts of which will appear in the next issue, were read.

STEREOSCOPIC VISION: BINOCULAR TEMPORAL SUMMATION

By R. EFRON

TACTILE LOCALISATION

By G. H. WRIGHT and C. R. E. HALNAN

SOME EFFECTS OF RESERPINE ON BEHAVIOUR IN THE RAT

By P. H. GLOW

THE ANALYSIS OF OPTOMOTORIC REACTIONS IN INSECTS AND CRUSTACEA

By B. HASSENSTEIN

A TEST OF THEORY OF SHAPE DISCRIMINATION IN OCTOPUS

By N. S. SUTHERLAND

TACTILE DISCRIMINATION IN OCTOPUS

By M. S. WELLS

SOCIAL INTERACTIONS IN DISCRIMINATION LEARNING

By P. KLOPFER

SOME PROBLEMS IN LOCALISATION OF HORMONAL ACTION ON THE C.N.S.

By R. WARREN

PROCEEDINGS OF THE SECTION OF ANIMAL BEHAVIOR AND SOCIOBIOLOGY OF THE ECOLOGICAL SOCIETY OF AMERICA

A meeting was held on 26th and 27th August, 1958, at the Department of Zoology, Kansas State College, Manhattan, with Dr. Martin W. Schein, Dr. A. M. Guhl, and Dr. J. T. Emlen in the Chair at the various sessions. Abstracts of the papers and films presented are given below.

REPRODUCTIVE BEHAVIOUR OF THE CHORUS FROG *Pseudacris nigrita*

B. S. MARTOF AND E. F. THOMPSON, JR.
Department of Zoology, University of Georgia, Athens, Georgia

Laboratory experiments showed that a female responds to the calls of a male by moving into contact with him. Clasping results and the female, now positively phototactic, moves to more open water where oviposition occurs. Experiments with hidden males eliminated the possibility of visual cues bringing the sexes together. Experiments with only a recording of a calling male showed that vocalisation was the sole source of directive stimuli. The reactions among males varied according to the density of the aggregation and to the amount of cover present. Under conditions of high population/cover density, the males moved about—much testing and tussling occurred as they attempted to clasp one another. At intermediate density, little or no testing resulted, but frequently a male remained motionless, but attentive, while a nearby male continued to call. After several minutes, the "defensive male" abruptly hopped away. At low density, no interactions occurred. (12 minutes).

THE EFFECTS OF ANDROGEN ADMINISTERED PRENATALLY ON THE BEHAVIOUR OF SPAYED FEMALE GUINEA PIGS INJECTED WITH ALPHA-ESTRADIOL BENZOATE AND PROGESTERONE

BY R. W. GOY, C. H. PHOENIX AND W. C. YOUNG
University of Kansas

Pregnant guinea pigs were injected with 1 mg. of testosterone propionate between days 10 and 27 and 1 mg. every 3 days thereafter. Fourteen of the female offspring were spayed when 30 to 90 days old. Beginning approximately the 90th day, varying quantities of α estradiol benzoate and 0.2 I.U. progesterone were injected. Behavioural responses were compared with those of five control females. Lordosis responses and male-like mountings were recorded.

Experimental females exhibited a shorter duration of heat and maximum lordosis, and a higher incidence of incomplete lordoses. Latency of heat was not altered. Experimental females did not display significantly more male-like mounting than controls.

The results suggest that testosterone given prenatally interferes, for the most part, with the expression of the lordosis component of adult female sexual behaviour. (15 minutes).

Supported by research grant M-504, from the National Institute of Mental Health of the National Institutes of Health, Public Health Service.

MODIFICATION OF SEXUAL BEHAVIOUR IN FEMALE GUINEA PIGS PRODUCED BY PRENATAL AND POSTNATAL TREATMENT WITH TESTOSTERONE PROPIONATE

By C. H. PHOENIX, R. W. GOY, A. A. GERALL and W. C. YOUNG
University of Kansas

Seventeen experimentally produced female pseudohermaphrodites with modified external genitalia and 11 normal females were used. Beginning 1 to 3 days after birth 9 pseudohermaphrodites and 7 normal females received daily injections of 500 γ testosterone propionate per 100 g. body weight. The remaining animals were not treated postnatally. Starting the second week subjects were placed with an oestrous female for 10 minutes each week and their masculine responses (nuzzling, mounting, "intromission," "ejaculation") were recorded.

Pseudohermaphrodites treated postnatally obtained higher weekly average male sex scores than normal females receiving androgen. All animals in these two groups displayed well oriented mounts and some "ejaculated." Normal females and pseudohermaphrodites not receiving postnatal treatment obtained low male sex scores. The data suggest that mounting was displayed by a greater proportion of untreated pseudohermaphrodites than normal untreated females.

Postnatal treatment of the normal female resulted in a sexual behaviour pattern more closely resembling that of the male. The significance of these findings will be discussed. (15 minutes).

Supported by research grant M-504 from the National Institute of Mental Health of the National Institutes of Health, Public Health Service.

THE EFFECT OF ADRENALECTOMY ON THE SEXUAL BEHAVIOUR OF CASTRATED MALE CATS

By MADELINE COOPER & L. ARONSON
Department of Animal Behavior, American Museum of Natural History, New York, N.Y.

After castration of sexually experienced male cats the occurrence of mating behaviour is variable but persists in some individuals for several years. We have investigated the hypothesis, often proposed, attributing this persistence to androgenic secretions of the adrenal cortex.

Sexual behaviour was observed in three groups of sexually experienced male cats: Group I—castrated; Group II—castrated and implanted with DCA pellets; Group III—castrated, adrenalectomized and implanted with DCA pellets. Group III was further subdivided into (*a*) castrated and adrenalectomized simultaneously as adults; (*b*) adrenalectomized and implanted with DCA as adults, permitted additional sexual experience and then castrated; (*c*) prepuberally adrenalectomized and implanted with DCA, subsequently permitted sexual experience and castrated as adults.

Analysis of frequency and duration of various elements of the sexual pattern revealed no significant differences among the three groups.

It is concluded that persistence of sexual behaviour after castration in experienced adult male cats cannot be attributed to androgens secreted by the adrenal cortex. (Illustrated, 2″ × 2″, 15 minutes).

This study was supported in part by grants from the Committee for Research in Problems of Sex, National Research Council, and from the National Institutes of Health.

MECHANISMS OF STIMULATORY AND INHIBITORY SEXUAL REFLEXES IN MAMMALS

By E. S. E. HAFEZ
Department of Animal Science, State College of Washington, Pullman, Washington

In the male, erection, penetration and ejaculation reflexes are controlled by neuro-motor and neuro-hormonal mechanisms as well as peripheral sensitivity (thermal and tactile). Favourable thermal sensation, pressure stimulus, anticipation, jealousy, displays and frustration

cause increase in ejaculatory thrust. Excessive stimulation causes excessive stimulation of sexual centres and subsequent protective inhibition. Inhibitory reflexes could be reinforced by repeated conditioning to unfavourable environments at short intervals. Tolerance against conditioned reflexes varies with the species, strain, individual and mental state. Inhibition could be easily released in visual conditioning. In the female, spontaneous and conditioned sexual reflexes are a result of auditory, visual, olfactory and tactile stimuli. Unusual placid reactions at copulation may affect conception as caused by epinepherine secretion. The hereditary factors affecting sex drive, copulatory patterns and estrus symptoms are discussed in relation to evolutionary trends and to climatic stressors. (15 minutes).

SELECTIVE FEEDING BY DUCKLINGS OF DIFFERENT SPECIES

By E. COLLIAS and ELSIE C. COLLIAS
Illinois College, Jacksonville, Illinois

Wild, incubator-hatched ducklings of ten species, during their first week, ate many daphnids, amphipods, various insects and other invertebrates, but little or no duckweed. Different species appear to specialise on different kinds of invertebrates, despite some overlap in diet. Thus, much of the natural diet consists of midge larvae in Ruddy ducklings, and of small snails in Blue-winged Teal. Such selective feeding was observed directly, in the laboratory, on exposing different species of ducklings simultaneously to various food organisms.

We observed feeding methods in nature to reflect diet differences; during the first week after hatching, Ruddy and Scaup broods fed mostly by diving, Blue-winged Teal broods by pecking and straining, while Redheads and Mallards often used all these methods.

This study was done at the Delta Waterfowl Research Station, Manitoba.* Traditionally good places for broods counted in the marsh were also richest in measured numbers of invertebrate food organisms. (Illustrated, 2″ × 2″, 15 minutes).

*Supported by a grant from the North American Wildlife Foundation and the Wildlife Management Institute.

FORAGING AND FOOD DISCRIMINATION OF THE KANGAROO RAT *(Dipodomys)*

By R. D. BURNS
Department of Zoology, Michigan State University, East Lansing, Michigan

Four species of Dipodomys (*D. deserti*, *D. panamintinus*, *D. agilis* and *D. merriani*) were observed in two series of experiments in order to evaluate the relative importance of the olfactory and tactile senses in food gathering.

The results of the bead-seed test indicated that beads with similar shapes as the seeds were placed inside the cheek-pouches along with the seeds. Individuals which sampled material by nibbling with the incisors and manipulating with the manus tended to discard the beads. Kangaroo Rats sampled material at the beginning of an experiment. If the first objects sampled were seeds, the remainder was placed inside the cheek-pouches without further testing, and beads were then placed in the pouches.

In the sand-seed experiments individuals were unable to locate seeds underneath 1-2 cm. of fine dry sand, but would readily pick up seeds upon the surface. They continued to forage for seeds where they had been exposed, but ignored groups of seeds under the sand. (Illustrated, 3¼″ × 4″ slides and 16mm. movies, 15 minutes).

EFFECTS OF EARLY FOOD DEPRIVATION UPON LATER CONSUMMATORY BEHAVIOR IN PUPPIES*

By O. S. ELLIOTT and J. A. KING

Behavior Division, Roscoe B. Jackson Memorial Laboratory, Bar Harbor, Maine

Young basenji and wirehaired fox terrier puppies were put on a deprived feeding schedule at an early period in development which was considered "critical" in the formulation of enduring character traits in dogs. Control puppies were fed twice as much food on schedule as the deprived puppies during a 3-week experimental period from four to seven weeks of age. At 13 weeks of age, both groups were tested (1) for food consumption after 24 hours deprivation and (2) for their social reaction to human beings.

Deprived puppies ate both significantly more food and at a faster rate than did the control puppies at 13 weeks of age. In their reactions to human beings, the deprived puppies received higher attraction scores and lower avoidance scores than did the controls.

The results can be interpreted in terms of food frustration, learning to eat rapidly, or response to a chronic physical deprivation. (Illustrated, 3¼″ × 4″, 15 minutes).

*Supported by Grant MH-123 from the National Institutes of Health, Public Health Service, and by the Ford Foundation.

SCHEDULED FOOD DEPRIVATION, RESPONSIVENESS, AND LEARNING IN THE YOUNG PUPPY*

By W. C. STANLEY

Behavior Division, Roscoe B. Jackson Memorial Laboratory, Bar Harbor, Maine

This study sought to answer two questions: (*a*) Does food deprivation increase the puppy's general and consummatory activity? (*b*) Do scheduled daily food deprivations show effects which might be attributed to learning?

From age 5 to 15 days, four basenji x cocker puppies were separated from their mothers 16 hours daily; four puppies were separated 8 hours; four puppies were not separated. The 16- and 8-hr. puppies were reliably more active and vocal after deprivation than before deprivation. Vigorous sucking of a human finger occurred only in 16-hr. puppies. Weight gain in the 16-hr. group was markedly depressed. However, weight gains in the 8- and 0-hr. groups were essentially identical until all puppies were returned permanently to their mothers. Then, the 16- and 8-hr. groups gained weight more rapidly than the 0-hr. group. The difference between the 8- and 0-hr. groups may be attributed to differential prior experience, hence, to learning (Illustrated, 3¼″ × 4″, 15 minutes).

*Supported by a grant from the Ford Foundation.

SOCIAL BEHAVIOUR OF DOMESTIC GOATS AND SHEEP: A COMPARATIVE STUDY

BY J. P. SCOTT

Roscoe B. Jackson Memorial Laboratory, Bar Harbor, Maine

A flock of goats of mixed ancestry was studied observationally and experimentally over a period of 12 years, while living under semi-natural conditions. With the following exceptions, systematic comparison shows that the behaviour patterns of goats and sheep are quite similar. (1) Ingestive behaviour—more browsing by goats. (2) Sexual behaviour—similar, but more intense in male goats. (3) Epimeletic behaviour—female goats leave newborn kids, which have a freezing reaction not found in lambs. (4) Allelomimetic behaviour—goats more independent, less tendency to follow a single leader. (5) Agonistic behaviour—greatest differences; pattern of butting different, male goats tend to round up females, alarm signal or "sneeze" present in goats. It is concluded that patterns of behaviour tend to be conservative in evolution, and comparisons are made with other ruminents. (Illustrated, standard lantern slides, 15 minutes).

HOW TO PREDICT WHAT AN ANIMAL WILL DO NEXT

S. A. ALTMANN

The Biological Laboratories, Harvard University, Cambridge, Mass., and National Institute of Neurological Diseases and Blindness, Bethesda, Maryland

What an animal does at any moment depends in part upon preceding behavioural events. Therefore, an attempt to maximise the accuracy of predictions of behaviour must take into account the probabilities of sequences of behaviour. In order to represent the complex sequences of events that occur among social animals, a mathematical model, based on communication theory, is introduced. Some advantages of the model over traditional methods of description are pointed out and some ramifications of the model are briefly described. The practicability of research based upon the model has been demonstrated by a study of social organisation in free-ranging rhesus monkeys. (15 minutes).

OBSERVATIONS ON THE BEHAVIOUR OF THE POMACENTRID FISH *Amphiprion percula*, COMMENSAL OF THE ANEMONE *Stoichactis*

BY D. DAVENPORT AND K. S. NORRIS

University of California, Santa Barbara College and Marineland of the Pacific

The process is described whereby an *Amphiprion percula*, unacclimated to the host *Stoichactis kenti* and newly introduced into an aquarium containing the host, effects its association.

Evidence is presented that the protection of the fish is at least in part effected by the secretion of a mucus from the skin of the fish which specifically raises the threshold of discharge of its host's nematocysts. This factor is not heat stable and is not present in the muscle of the commensal fish. It is effective in preventing discharge of nematocysts from isolated tentacles under mechanical stimulation, but does not alter the threshold of discharge under electrical stimulation.

The physiological effect upon each other of contact between the partners is discussed. (Illustrated, 2″ × 2″, 15 minutes).

THE INFLUENCE OF SOCIAL DOMINANCE ON EXPLORATORY BEHAVIOUR: A COMPARISON OF SOME FISHES AND ARTHROPODS

F. D. KLOPFER

Department of Psychology, State College of Washington, Pullman, Washington

The exploratory behaviour of six species of benthic marine fishes, one freshwater, one terrestrial and one marine arthropod species is compared. Individuals differing in social dominance were tested alone and in pairs in a limited relatively homogeneous tank.

The following conclusions seem justified:

1. Differences among species represent schooling vs. territorial characteristics.
2. Pairings of schooling fish vs. "alone" results in increased rate and magnitude of exploration.
3. With pairings in other species,

(*a*) Dominant animals explored more, sooner, and defended a larger territory away from the starting point;

(*b*) Submissive animals explored less, later, and defended a small territory near the release point;

(*c*) Both groups explored more rapidly, were more "emotional" and responded sooner to food when paired than when alone.

In tests where shelters were provided, dominant animals spent less time in shelters than submissive, and less when paired than when alone.

Results were discussed in relation to theoretical formulations of drive and anxiety. (Illustrated, 3¼″ × 4″).

EFFECTS OF ISOLATION AND SOCIAL CONTACT UPON THE DEVELOPMENT OF AGGRESSIVE BEHAVIOUR IN THE SIAMESE FIGHTING FISH, *Betta splendens*

By J. C. BRADDOCK and ZORA I. BRADDOCK

Department of Zoology, Michigan State University, East Lansing, Michigan

Forty individuals were selected at random from a large litter of *Betta splendens* at three days post-hatching. Twenty of these were physically and visually isolated at this time. The other twenty were allowed to develop as a group. The grouped individuals were tested in pairs at 56, 63, 70, and 77 days post-hatching. Certain of the isolated fish were observed as controls at each of these intervals. The observations were repeated using 20 fish from another litter, but these were paired only once at the age of 77 days.

Such data were recorded as the elapsed time before the first social reaction, the nature of that reaction, relative frequencies of infantile and adult behaviour patterns, and frequencies and nature of fights. In general it was found that individuals performed in accordance with their ages rather than their prior experience insofar as the ability to perform specific acts was concerned. The frequencies and facility with which the acts were performed indicated some effect of learning as a result of contact with other individuals.

THE "PUSH-UP" BEHAVIOUR OF *Sceloporus*

By C. C. CARPENTER

Department of Zoology, University of Oklahoma, Norman, Oklahoma.

No abstract of this paper was available at the time of going to press. (Illustrated, 16 mm. movie, 15 minutes).

AGONISTIC BEHAVIOUR OF THE COMMON GRACKLE, *Quiscalus quiscula*, ANALYZED BY BLAUVELT MOTION PICTURE TECHNIQUE

By R. W. FICKEN

Laboratory of Ornithology, Cornell University, Ithaca, New York

Motion pictures of agonistic behaviour of Common Grackles, *Quiscalus quiscula*, were taken at baited areas with a Bell & Howell Time Motion No. 70 camera. In some cases attendant vocalisations were recorded. The data were studied using a technique developed by Dr. Helen Blauvelt. The film was projected with a special Bell & Howell Projector which enabled frame by frame analysis. Observations were made on an "analysis sheet" and the data obtained were then transferred to a "simo-chart" which was designed to show the exact interactions in time and space of two or more individuals. In this way some valuable insights concerning the signal function of the displays were obtained. These displays were analysed in terms of the underlying tendencies producing the displays. Comments on the probable evolutionary derivation of these ritualised motor patterns were included.

(Illustrated 16 mm. motion pictures, 15 minutes).

THE TIME OF PAIRING OF STARLINGS

By D. E. DAVIS

Johns Hopkins School of Hygiene and Public Health, Baltimore, Maryland

Starlings (*Sturnus vulgaris*) begin to defend a nest hole in the fall. Sub-adult (aged 5 months) as well as adult males will fight other males to protect their site. A series of observations was organised to determine when during the year pairing occurs. Two methods were used: (1)

observations of colour-banded birds at nest boxes (about 350 hours from October to May); (2) counts of the number of singles, doubles, triples, etc., arriving in the morning from the roosts. The results gave no indication of pairing until April. In no case was a male and female associated at a nest box for more than a few days. In the middle of April, however, pairs of colour-banded birds were regularly seen at boxes, feeding on the ground, and flying off to the roost together in the evening. The counts of birds arriving at dawn showed that 20-25 per cent. of the groups were doubles from September until April 15th. At that time the percentage increased to 40 and then dropped on April 22nd to 20 per cent. and remained about that level. The first egg (in 23 nests) was laid April 19th. It is concluded that pairing occurs about 4 days before the first egg is laid. (Illustrated, 2″ × 2″, 15 minutes).

PRELIMINARY OBSERVATIONS ON COLONIES OF BIG BROWN BATS

ELIZABETH SMITH AND W. GOODPASTER
Pennsylvania State University, Erie, Pennsylvania

In the three state area in the vicinity of Cincinnati, all but one of the bat colonies found are composed of big brown bats, *Eptesicus fuscus*. The behaviour of these bats shows several differences from that shown by colonies of little brown bats, *Myotis lugifugus*. Most striking is the apparent non-migratory behaviour of the big brown bats. Growth changes during the year have been observed in individual banded bats. Other differences have been noted in homing ability, percentage recaptures, and sex ratios. (15 minutes).

HOMING IN BATS*

HELMUT C. MUELLER
University of Wisconsin
(Introduced by John T. Emlen, Jr.)

Experiments in 1957 confirmed prior results (Mueller & Emlen, 1957, *Science*, **126**, 307). Bats home rapidly over long distances (up to 60 miles in 3 hours) and blindfolding has no effect on the performance of displaced bats. In an experiment designed to test directional effects 25 bats were released 5 miles from the home roost in each of the 4 cardinal directions. Those that returned before midnight were re-released the same night in the opposite directions. Returns from the re-release were significantly poorer than those from the original release. Returns from the West re-release were significantly better than those from the other directions. An additional 25 bats were released East and returnees from this group were re-released East. Homing performance was about the same for these two releases. (15 minutes).

*Aided in part by a grant from the Wisconsin Alumni Research Foundation.

AN HYPOTHESIS CONCERNING THE MECHANISM OF HOMING OF BATS

J. W. TWENTE, Jr.
Department of Zoology, University of Utah, Salt Lake City, Utah

Observations indicate that bats may locate caverns through sounds made by other bats therein. It is also suggested that those individuals released beyond their normal, familiar home range, even though blind-folded, may return to the cavern of original capture by following sounds made by other flying individuals of the same species. Even those individuals flying over unfamiliar terrain may be guided, over a period of time, by different individuals with overlapping home ranges and the experimentally released bats may then eventually, by chance, enter into the familiar territory of the "home" cavern. (10 minutes).

BEHAVIOURAL DEVELOPMENT IN TWO SUBSPECIES OF *Peromyscus maniculatus**

J. A. KING AND NANCY SHEA
Behavior Division, Roscoe B. Jackson Memorial Laboratory, Bar Harbor, Maine

The behavioural development of *P. bairdii* and *P. gracilis* was measured by a swimming test and an escape from shock test given to the mice from 10 to 30 days of age. Longitudinal and cross-sectional samples of 10 mice in each of seven groups (total 280 mice) were taken from a laboratory colony.

The performance curves of *bairdii* in the swimming test were steeper and reached a higher asymptote than those of *gracilis*. Cross-sectional groups behaved similarly to the longitudinal groups at the same age. In escape from shock, *bairdii* remained motionless on the escape pan, while *gracilis* repeatedly leapt from the escape pan back onto the electrified grid.

The rapid sensory-motor development of *bairdii* enables them to mature behaviourally at a faster rate than *gracilis*. Subspecific differences in response to noxious situations appear between 14 and 18 days of age and arise independently of prior experience. (Illustrated, $3\frac{1}{4}'' \times 4''$, 15 minutes).

*Supported by Grant MH-123 from the National Institutes of Health, Public Health Service.

HOPPING BEHAVIOUR IN MICE OF PRE-WEANING AGE

ETHEL TOBACH, T. C. SCHNEIRLA, B. SANG, P. GOLD, K. STEELE AND R. WORTIS
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Nondirected hopping has been observed in mice before weaning. Hopping responses to the following stimuli were studied in 299 B Albino/C mice 12 to 21 days of age: (1) light (steady and intermittent); (2) buzzer (steady and intermittent); (3) airstream (on or near the animal); (4) intermittent shadow and (5) intermittent light plus airstream on animal. Two control groups were also studied: (6) observations of individuals and (7) observations of groups of five. At 25 days of age, animals were subjected in groups on five consecutive days to air-blasts. More hopping responses were shown by animals stimulated by buzzer, airstream and light plus airstream than by any other groups. Twelve to 15 day old mice hopped less than 16 to 21 day old animals. Control animals observed individually hopped more than those observed in groups. More convulsions during air-blasts were seen among animals stimulated by the shadow and by light plus airstream than among other groups. No relationship was demonstrated between hopping before weaning and convulsion during air-blast. (Illustrated, $2'' \times 2''$, 15 minutes).

ATTEMPTS TO INFLUENCE THE SEXUAL BEHAVIOUR OF SOCIALLY ISOLATED MALE GUINEA PIGS*

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AND HELENE W. DUNNING
Department of Psychology, University of Kansas, Lawrence, Kansas

Each of 6 new-born male guinea pigs was placed with a lactating female prior to total isolation at 10 days of age. Four control animals were raised with litter mates. Three control but only one isolated male displayed a mature copulatory pattern during the first 5 mating tests beginning at 60 days of age. The remaining 5 isolated animals exhibited no mounts with clasps although they showed sexual arousal as indicated by circling and nuzzling. These findings confirm previous studies from this laboratory. Isolated animals also manifested a characteristic head-shaking and non-directed hyperexcitability. The following experimental manipulations did not significantly alter the isolated animals' behaviour: (1) extension of mating tests from 10 to 20 minutes duration; (2) a 60-day test-free interval; (3) 20 mg. of caffeine/kg; (4) 0.1 cc. 50 per cent. ethyl alcohol given five minutes before the test; (5) 0.125 mg/kg. reserpine given for two days before the test.

*The work was supported by research grant M-504, National Institute of Mental Health, N.I.H., U.S.P.H.S., administered by Dr. William C. Young.

FIGHTING IN YOUNG AND MATURE OPOSSUMS

L. T. EVANS
Albert Einstein College of Medicine

The fighting posture of the young opossum is indicated by the uptilted snout and widely opened mouth. This pattern is derived from the open-mouth response which the animal makes to the sudden impact of any tactile, odorous, auditory or visual stimulus, from the moment it emerges voluntarily from the pouch until old age overtakes it. This threat posture serves as the "releaser" for nearby opossums to open their jaws in the same fashion. Any stimulus at this moment of tension releases a swift, slashing bite and a return to the alert but immobile threat posture. The actual bite may be delivered in 1/16th second and is directed mostly at the snout of adversaries, although fatal wounds are sometimes suffered.

The adult male also slashes downward, penetrating the hide of its rival with the relatively huge and deeply rooted upper canines. The lower jaw then closes upon the victim which is shaken vigorously. To one who has studied the patterns of lower vertebrates, this opossum technique bears a striking resemblance to the intimidatory display of the snapping turtle, alligator, lizard or serpent. (15 minutes).

THE ANALYSIS OF ANIMAL SOUNDS

D. J. BORROR
Ohio State University

Accurate information on animal sounds may be of considerable value to taxonomists and students of animal behaviour.

To analyse an animal sound, we need to determine the frequencies of the various notes, their relative loudness, and their rhythm. Most of these characteristics can only be estimated by ear, but electronic instruments are now available which can measure them with considerable accuracy.

Most instrumental analyses of animal sounds are made with either an oscillograph or a sound spectograph from recordings. The sound spectograph is an instrument that makes graphs of sounds, portraying time on the horizontal axis and frequencies on the vertical axis. The use of this instrument is described, and graphs of the songs of several bird species are shown to illustrate the sort of information that can be obtained. Features that make a song musical or nonmusical are pointed out, and some practical applications of sound spectograph data are suggested.

SOUND PRODUCTION AND COMMUNICATION IN INSECTS

R. D. ALEXANDER
University of Michigan

Sound communication in insects can be discussed under two headings: (1) long-distance signalling, or communication from outside the range of other senses, (2) and signalling among individuals in close proximity. Long-distance signals function primarily in bringing adult males and females together, and consequently a high degree of specific distinctiveness and complexity in song rhythms, and of sensitivity in auditory organs, has evolved. Congregation occurs in several different ways.

In close proximity sound signals may function in courtship, in fights between males, in escape from predators, and in other situations. Intraspecific structural modifications with change in situation are often remarkable. Interspecific distinctiveness is less evident, though it may be marked among closely related species which initially congregate in the same habitat niches.

Experimental work recently published and in progress continues to stress the significance of understanding of acoustical behaviour in studies on the systematics, ecology, and evolution of a wide variety of insects.

UNDERWATER COMMUNICATION IN FISHES

W. N. TAVOLGA
American Museum of Natural History, N.Y.

Resulting from the widespread use of underwater sound detection equipment during the last war, much attention has been attracted to the study of sound production by marine organisms. Most of the early reports on fishes in this regard were fragmentary. Recently, intensity and frequency measurements were made and the sound makers have been identified. Most fish sounds are produced with the aid of the swim bladder, but other mechanisms have been described. Many of the sounds are probably correlated with feeding, territorial defence, fright reactions, and, possibly, schooling. However, the behavioural significance in most instances is not known. Sounds that are clearly related to a specific behaviour are described from species of the families Gobiidae and Blenniidae. Here only the males produce the sounds and only during courtship behaviour. Both sexes respond to playback of these sounds and to artificial imitations.

Aided by the Office of Naval Research Contract No. NR 163-322.

THE ONTOGENY OF VOCALIZATIONS IN BIRDS

W. E. LANYON
American Museum of Natural History, N.Y.

Investigations of the ontogeny of animal sounds have recently achieved a welcome degree of objectivity, largely as the result of technological advances in sound recording and analysis. In no group has progress been greater than with birds, though even there the number of species for which there are meaningful data is still small. Some aspects of these studies are: the basis for the variability of given vocal patterns and the stereotypy of others; the sequential pattern of ontogeny, and the identification of precursors and derivatives; the age at which vocal patterns become manifest; the concept of a "critical learning period"; the possibility of latent manifestation of vocalisations; the irreversability of vocal patterns; the size of vocal repertoires of given species; and the endocrine influence on the ontogeny and manifestation of vocalisations. A combination of observational and experimental procedures involving free-living birds, individuals reared from the nestling stage, and others reared from the egg has been most productive.

(Illustrated, 2″ × 2″, 20 minutes).

FUNCTIONS OF ANIMAL SOUNDS: AN ECOLOGICAL CLASSIFICATION OF ANIMAL COMMUNICATIONS

N. E. COLLIAS
Illinois College

Present knowledge of animal communication by sounds indicates considerable variety and specificity in the information than can be transmitted. However, the various sound-signals fall readily into five broad ecological categories related to (1) food, (2) predators, (3) sexual behaviour and related fighting, (4) parent-young interrelations, and (5) aggregation and group movements. This general classification was first worked out in detail for birds, but also applies to other animals.

The same sound may have more than one specific meaning depending on context, thus, various unfavourable conditions elicit distress calls by chicks and baby ducklings, whereas relief from these conditions inhibits distress calls and stimulates pleasure notes.

Sounds with similar function in different animals frequently seem to be characterised by certain common properties. Alarm cries are often harsh, prolonged and high-pitched, threat sounds often harsh and relatively low-pitched, while attraction calls to the young by the parent are often soft, low-pitched, brief and repetitive notes.

BIRD SONGS AND MATE SELECTION

P. MARLER
University of California

It is widely accepted that many bird songs aid in reproductive isolation of the species, though few experimental confirmations of this hypothesis have been made. If we accept this provisionally, certain corollaries follow which can be tested. The need for specific distinctiveness will have two effects.

First it will result in adaptations of song form, the precise nature of which will be affected by the predominant sounds in the environment, especially the songs of other birds. Geographical variation of song may provide a means of assessing the kind of effects which changes in the sound environment can have.

Second, it will tend to encourage stereotypy in the parameters of the song used in specific recognition. Study of intra-specific variation in song should throw light on which of the parameters are specific. The more variable aspects must have other functions, and at least one of these is probably the facilitation of individual song recognition.

BOOK REVIEWS. Owing to pressure on space, the book reviews scheduled for this issue have been held over until the next.

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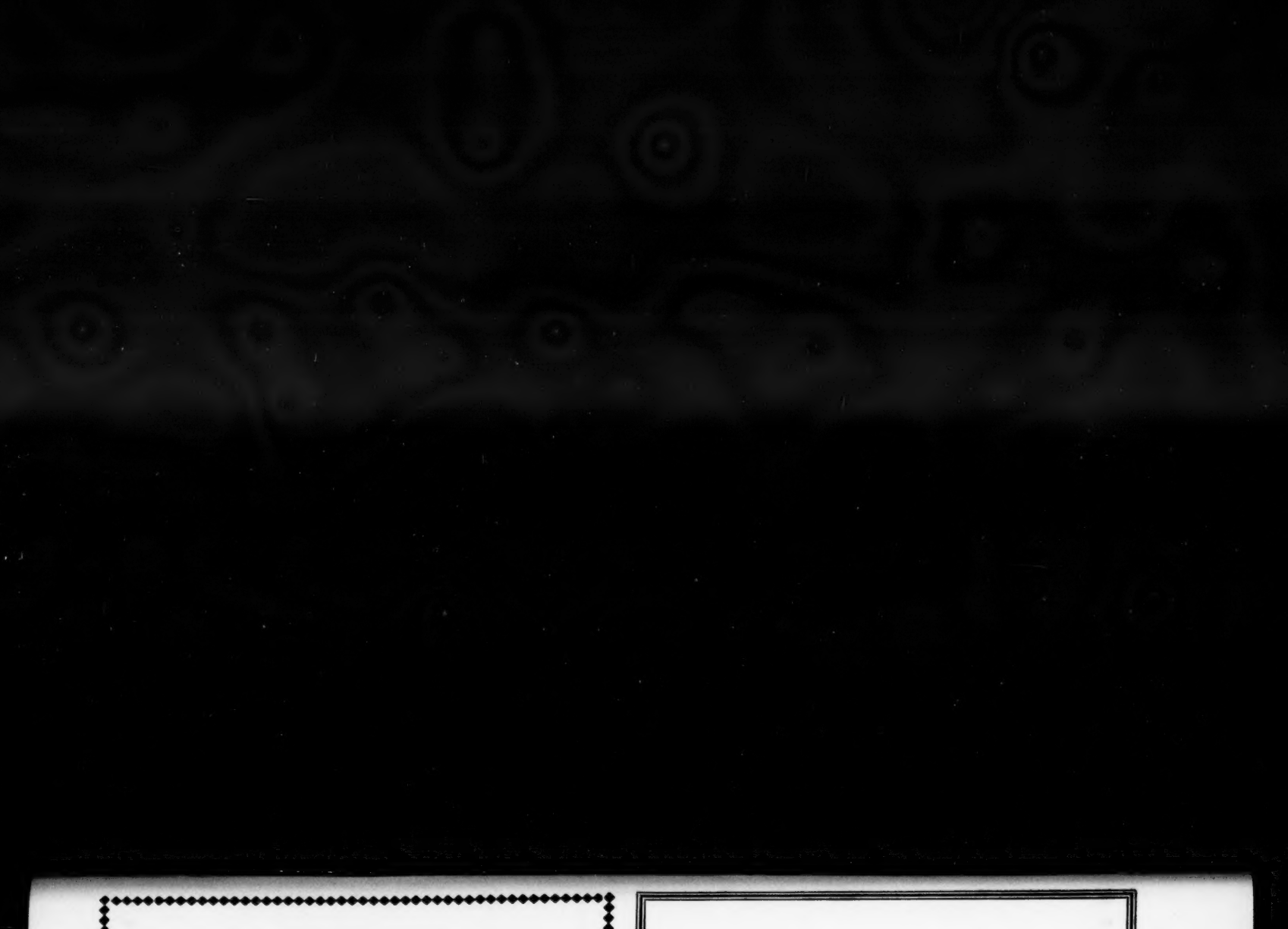
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